Somatosensory perception of the hands and feet

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A THESIS SUBMITTED FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY (PhD)

BIRKBECK, UNIVERSITY OF LONDON

2020

Originality Declaration

I, Kelda Manser-Smith, declare that the entirety of work in this thesis is my own. Where information has been derived from other people's work or ideas, this is clearly indicated.

The thesis includes research that appears in the following articles:

Chapter 2:

Manser-Smith, K., Tamè, L., & Longo, M. R. (2018). Tactile confusions of the fingers and toes. *Journal of Experimental Psychology: Human Perception and Performance, 44*(11), 1727-1738.

Chapter 3:

Manser-Smith, K., Tamè, L., & Longo, M. R. (2019). A common representation of fingers and toes. *Acta psychologica, 199*, 102900.

Chapter 8:

Manser-Smith, K., Romano, D., Tamè, L., & Longo, M. R. (2020). Fingers hold spatial information that toes do not. *Quarterly Journal of Experimental Psychology*, 1747021820960094.

Abstract

Somatosensory perception of the body has been shown to be systematically biased. This thesis aims to contribute to knowledge of our somatosensory perception of our bodies, and how these perceptions are systematically distorted. In particular I investigated similarities and differences between the hands and feet. My results showed that a number of different somatosensory processes are systematically biased across both the hands and feet, for example tactile localisation of the digits, localisation across the palm and dorsum, and distance perception. Biases were mostly consistent in their patterns across the hands and feet. Differences found between the hairy and glabrous skin surfaces on each body part were reflected in the other body part, as were individual differences in individuals' response patterns. This suggests that despite the differences in modern use and physical structure of the hands and feet, deep functional connections remain between the somatosensory representations of these body parts, from their common genetic development. I suggest that these findings provide evidence for a common, abstracted representation of the hands and feet, such as has been previously proposed by other researchers. Finally, I showed that there remain some differences in how somatosensory information is processed by the fingers and toes – tactile stimuli applied to the fingers more easily distracts from identifying touches to the toes than vice versa, and representations of the fingers contain spatial information that the toes do not. These findings show that despite the connectedness of somatosensory representations of the hands and feet, differences in use can induce plasticity in their representations.

Acknowledgements

Thank you to the Economic and Social Research Council for funding my research.

I am of course extremely grateful to my supervisor Professor Matthew R. Longo for supporting me throughout my PhD. His infinite patience and help have made the past three years much more enjoyable than they otherwise might have been! I would like to thank Dr Luigi Tamè for all the help and support he has given me throughout my PhD, especially all the hours spent staring at MATLAB trying to figure out what the hell was going on. I would also like to thank my other co-author and collaborator Dr Daniele Romano for his contribution to my work. I am particularly grateful to all the past and present members of the Body lab for creating such a friendly and supportive working environment, Raffaele, Renata, Klaudia, Lara, Elena Azañón, Elena Amoruso, Olga, Kasia, and others. I would also like to thank the students and volunteers who worked with me and helped collect data, Olivia and Xue.

Finally, I have to thank my friends and family. To my Dad, Nan, Camilla, Ashleigh, and Chris's family – thank you for your constant support and reassurance. And Annie and Chris, the best team I could ever ask for, I love you guys.

This research was supported by a grant from the Economic and Social Research Council (ESRC).

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Chapter 1: General Introduction

1.1. Introduction

For the most part, we take for granted our ability to localise touch on the body. Moreover, we assume that we can do this to a high degree of accuracy. To know something like the back of your hand is to know something intimately. However, it appears that this saying does not hold true for our sense of touch. Not only on the back of the hand (Longo & Haggard, 2011; Mancini, Longo, Iannetti, & Haggard, 2011), but on the forehead (Fiori & Longo, 2018; Longo, Ghosh, & Yahya, 2015), arms (Green, 1982; Le Cornu-Knight, Longo, & Bremner, 2014), and legs (Green, 1982; Stone, Keizer, & Dijkerman, 2018), to name just a few, we systematically misrepresent the structure of the body through touch.

A large amount of the literature in this field has focused on the hand, documenting consistent biases in our somatosensory representation of the hand. These findings are interesting given that biased hand representations are involved in carrying out skilled motor actions that require accurate tactile feedback (Dang & Allen, 2014; Jones & Piateski, 2006). Considerably less research has investigated somatosensory representations of the feet. Comparisons between the hands and feet are particularly intriguing as the hands and feet are serially homologous structures, meaning that they are share a common genetic origin (Lewis, 1989; Rolian, Lieberman, & Hallgrímsson, 2010), and number of features such as their overall structure (Lewis, 1989). Despite this, throughout human evolution the hands and feet have evolved to be quite different in

both their forms and uses, and therefore may differ considerably in their somatosensory representations.

Another interesting aspect of the somatosensory literature focused around the hand is the comparison of tactile perception across the hairy and glabrous skin surfaces. Both the hands and feet have a hairy and glabrous skin surface on their alternate sides (Lewis, 1989), although the properties of the homologous skin surfaces on each of these body parts are not the same, for example in mechanoreceptor density and distribution (Ackerley, Carlsson, Wester, Olausson, & Backlund Wasling, 2014; Hennig & Sterzing, 2009; Johansson & Vallbo, 1979; Kennedy & Inglis, 2002). As such, somatosensory representations of the two skin surfaces across both body parts may also differ, depending on the origin of these representations.

In my thesis I investigate somatosensory representations of the hands and feet, and how they are systematically distorted in healthy adults. I am particularly interested in how distortions of somatosensory representations of the hands and feet are similar or different, and what this can tell us about the origins of these biases.

1.2. Similarities and differences of the hands and feet

In the first section of this chapter I will compare the physical structure of the hands and feet, such as their bone structure and mechanoreceptor properties of the hairy and glabrous skin surfaces. I will describe how the divergent use patterns of the hands and feet of our evolutionary ancestors led to physical changes of the hands and feet. In the second section I will discuss how the physical nature of the hands and feet are reflected in the somatosensory mental representations of these body parts, looking at

behavioural and neurophysiological evidence. I will introduce a number of experimental paradigms that are used in my own research, and describe how my research comparing the somatosensory representations of the hands and feet can further our understanding of mental representations of the body.

1.2.1. Physical comparisons

The hands and feet are serially homologous structures, meaning that the underlying genetic program of these structures are of the same phylogenetic descent, but are expressed in different places during development (Lewis, 1989; Rolian et al., 2010). However, identical genetic programs do not necessarily mean that these structures are identical, as genetic programs can be altered by phenotypic traits during development, brought about by divergent specialisations (Lewis, 1989). Phenotypic covariation is very high between the hands and feet, suggesting that these structures co-evolved throughout human development, only diverging at a late stage in our evolutionary process (Rolian, 2009; Rolian et al., 2010).

Compared to great apes, human feet are characterised by the longitudinal arch, shorter toes, as well as less flexibility of movement between the toes (especially the non-opposable hallux [Holowka & Lieberman, 2018], Fig. 1.1). These changes may have initially occurred as we moved away from arboreal and towards terrestrial feeding, reaching for food from the ground instead of from the trees (Hunt, 1994). Following this adaptation, further exaggeration of these traits likely facilitated bipedal walking (Holowka & Lieberman, 2018; Hughes, Clark, & Klenerman, 1990). Short toes reduce mechanical work of the foot, therefore reducing metabolic cost and fatigue when

running over long distances (Rolian, Lieberman, Hamill, Scott, & Werbel, 2009). Pressure is distributed unevenly in favour of the big toe and inner side of the foot (Napier, 1967), supporting that the larger first toe evolved to improve balance in bipedal locomotion (Chou et al., 2009). Increased stiffness and mobility of the longitudinal arch in humans compared to apes helps the foot generate more power during push-off, also aiding long-distance walking or running (Holowka, O'Neill, Thompson, & Demes, 2017a). Through this process we lost the prehensile grasp of the toes needed by the great apes for arboreal locomotion (Holowka & Lieberman, 2018).

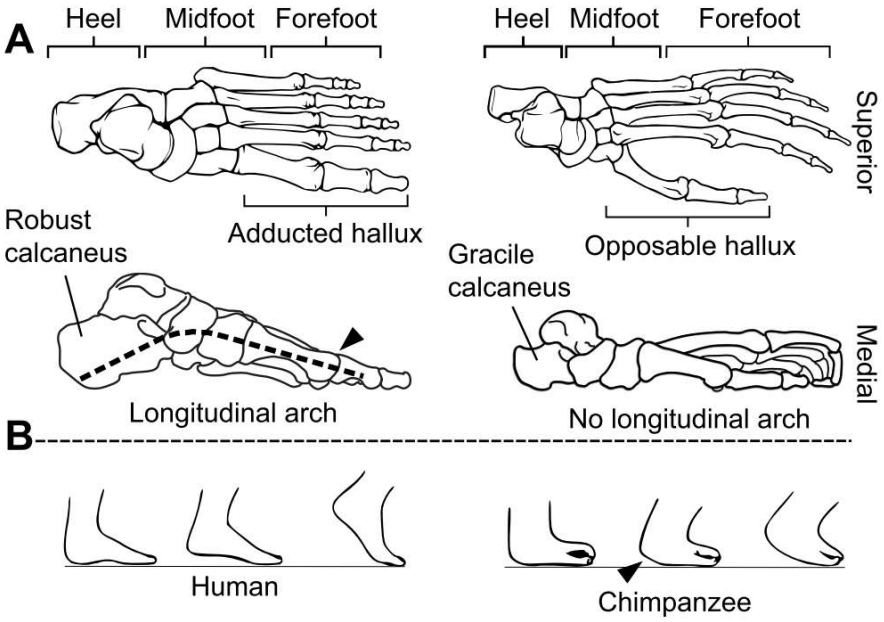

Figure 1.1. Comparison of the structure of chimpanzee and human feet. As can be seen in (A), two of the defining differences between human and primate feet are the change from opposable to adducted hallux, and development of the longitudinal arch. (B) shows how the stiff longitudinal arch allows the human foot to act as a lever, lifting both the heel and midfoot of the ground simultaneously, whereas the chimpanzee only lifts the heel during push-off. Image source: Holowka & Lieberman (2018, p. 2).

While the selection process of phenotypic changes for the toes was substantially stronger than for the hands, it is suggested that these changes led to parallel phenotypic changes in the hands, facilitating the emergence of stone tool technology (Rolian et al., 2010). Napier (1967) suggests a less direct link between bipedalism and the emergence of tool use, suggesting that the evolution from quadrupedal to bipedal walking only contributed as the hands became free to use while walking. Similarities and differences in the somatotopic representations of the fingers and toes in humans and primates may shed more light on the origins of these functions. Both primates and humans have independent representations of each finger, but while the representations of all the toes are fused in primates, the representation of the big toe is separate in humans (Hashimoto et al., 2013). Hashimoto and colleagues suggest that this indicates the development of dextrous fingers occurred before our evolutionary bifurcation from our primate ancestors (and so tool use may have evolved before bipedal walking), whereas the differences in representations of the toes occurred only afterwards.

The result of the co-evolution of the hands and feet is that there are a number of physical similarities between these two body parts. The types and numbers of bones in the hands and feet are identical, and while they maintain a somewhat similar bone structure they do differ in overall size and shape (Lewis, 1989; Owen, 1849/2008). However, it still remains that the hands and feet both have five digits (Lewis, 1989), as well as hairy and glabrous skin on their alternate sides (Lewis, 1989; Mountcastle, 2005).

As well as the obvious physical differences between the hands and feet in their overall size and shape, there are less obvious differences in the skin structure. On the

glabrous skin surface of the hand, mechanoreceptor density increases in a proximo-distal direction, with least sensitivity at the base of the palm, and the most at the fingertips (Johansson & Vallbo, 1979; Weinstein, 1962). While Pacinian (PC or rapidly-adapting type 2, RA2) and slow-adapting type 2 (SA2) receptors were evenly distributed across the glabrous skin area, rapid adapting type 1 (RA1) and slow-adapting type 1 (SA1) receptors accounted for the increase in density towards the fingertips, suggesting that these receptors play a main role in spatial acuity (Johansson & Vallbo, 1979). SA1 cells are sensitive to edges, corners and curvature, as well as providing information that forms the basis of texture perception (Johnson, 2001). RA1 cells are sensitive to velocity depression of the skin (indicating pressure on the skin surface), information that it critical in grip control and detection of motion of objects across the skin surface (Johnson, 2001). SA2 and RA2 cells are deeper within the epidermis, and provide information somatosensory information related to the entirety of the hand (Johnson, 2001). For example, the RA2 cells are sensitive to vibrotactile stimuli, providing the basis for tactile perception while using tools, and SA2 cells provide a neural image of skin stretch over the entire hand (Johnson, 2001).

Unlike the glabrous skin surface of the hand, the hairy skin surface does not contain RA1 cells, instead containing myelinated, rapidly-adapting hair and field mechanoreceptive afferents, and unmyelinated C-tactile (CT) afferents (Ackerley et al., 2014; Vallbo, Olausson, & Wessberg, 1999; Vallbo, Olausson, Wessberg, & Kakuda, 1995). Therefore, the hairy skin of the body has both fast-conducting, myelinated Aβ fibres (RA2, SA1 and SA2) and slow-conducting, unmyelinated CT fibres (Ackerley et al., 2014). All myelinated afferents also have a much lower density on the hairy than the

glabrous skin (Ackerley et al., 2014; Provitera et al., 2007), reflecting lower sensitivity on this body part. However, SA1 and SA2 receptors are particularly important for the hairy skin surface of the hand, to provide feedback about the hand position (through the stretch of the skin across the wrist joint and hand dorsum), which is important for proprioception and motor control (Eden, 1992).

On the glabrous skin surface of the feet, there are fewer SA receptors than on the glabrous skin surface of the hand (Johansson & Vallbo, 1979), but a much larger proportion of RA receptors than on the glabrous skin of the hand (Kennedy & Inglis, 2002). As RA cells are sensitive to pressure, there is likely a higher number of these cells in the glabrous skin of the foot as pressure sensitivity is an important function in gait control and balance (Inglis, Kennedy, Wells, & Chua, 2002). As well as differences in the number of each type of receptor, activation thresholds on the glabrous skin of the foot are significantly higher than those found for the glabrous skin of the hand (Kennedy & Inglis, 2002). This was true for RA receptors, but particularly pronounced for SA1 and SA2 receptors (Kennedy & Inglis, 2002). Higher activation thresholds of nearly all receptors on the glabrous skin of the foot reflect the large amount of downward force placed on the foot during locomotion, especially for the heel (Hennig & Sterzing, 2009; Napier, 1967). Inglis et al. (2002) specify that across the glabrous skin of the foot, psychophysical vibrotactile thresholds are lower in the ball of the foot and the arch of the sole than in the heel and toe regions, indicating that although the ball of the foot also receives a lot of downward force during locomotion, it is important that this region also remains sensitive to vibrotactile information.

As for the hand, the hairy skin surface of the foot was much less sensitive than the glabrous skin surface, especially for vibration detection, showing the importance of the palmar surface of both body parts for their respective uses (Hennig & Sterzing, 2009). On the hairy skin surface of the foot and the lateral border of the calf (i.e. the ankle) there were a larger proportion of SA receptors, including a third type of SA receptor (SA3) that is not found on the glabrous skin (Kennedy & Inglis, 2002). Differences in mechanoreceptor type and density across the hairy skin surface of the foot reflect their important use for monitoring stretch of the skin, which gives feedback of ankle position and movement of the ankle and foot (Kennedy & Inglis, 2002), in the same way as previously described over the hairy skin of the wrist.

In this section I have described the physical similarities and differences between the hands and the feet, and how they came to be throughout our evolution. In the next section I will describe how these similarities and differences may relate to the somatosensory representations of these two body parts.

1.2.2. Psychological comparisons

As mentioned in the very first section of my thesis, a large amount of the literature on somatosensory distortions in body representation has focused on the hands. While the physical similarities and difference between the hands and feet have been well-documented, less research has investigated how these similarities and differences are reflected on a psychological and neurophysiological level. In my research I aimed to investigate what traits of somatosensory hand representation are shared between the hands and feet, and which are not. I investigated this over a variety of somatosensory

functions, such as tactile localisation of the individual digits and tactile size perception. In the following section I will discuss the results of these studies that were performed on the hands, and present evidence as to why results may be similar or different on the foot.

1.2.2.1. Tactile localisation and the primary somatosensory cortex

The somatotopic organisation of the primary somatosensory cortex (S1) in the brain has been well-established, being first mapped over 100 years ago in primates by Leyton and Sherrington (1917) and later in humans by Penfield and Boldrey (1937). They reported that each body part of the contralateral body side is represented at a specific position in the postcentral gyrus, and described the cortical magnification of each body part (demonstrated in the somatosensory homunculus). They also showed that the fingers are represented separately from each other, with the representation of the thumb being larger compared to the other fingers (Penfield & Boldrey, 1937; Penfield & Jasper, 1954). Now several studies have described more fine-grained finger somatotopy in S1, with the fingers ordered along the medio-lateral axis of the postcentral gyrus (Fox, Burton, & Raichle, 1987; Kolasinski et al., 2016; Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2014; Schweizer, Voit, & Frahm, 2008). Modern studies have also confirmed the cortical magnification found by Penfield and colleagues across the fingers (excluding the thumb [Duncan & Boynton, 2007]), and shown that receptive field (RF) size increases along the rostro-caudal direction in S1, exhibiting a higher degree of response selectivity (Kolasinski et al., 2016). Considerably fewer studies have investigated toe somatotopy in S1. Akselrod et al. (2017) showed that the toes are still ordered sequentially in S1, with a similar pattern of cortical magnification from the first

digit (thumb/big toe) to the fifth. However, the toes are possibly ordered along the rostral-caudal axis of the postcentral gyrus, in contrast to the fingers along the medio-lateral axis. The distinct representations and somatotopic organisations of the fingers and toes may play an important role in differences in their somatosensory perception.

One line of research in somatosensory perception has investigated tactile localisation of the fingers. In this research, touches are applied to the individual fingers and participants are asked to localise the touch, sometimes to an individual finger, or to specific points on the finger. Tactile localisation of the fingers is generally quite accurate, given the fingers have a small point localisation sensitivity (Schweizer, Maier, Braun, & Birbaumer, 2000; Weinstein, 1962). However, when localising stimuli close to the sensitivity threshold of the fingers a characteristic pattern of mislocalisations emerges. Mislocalisation of touch on the fingers is more frequent on to neighbouring than to distant fingers (Braun et al., 2011; Braun, Ladda, et al., 2005; Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001; Schweizer et al., 2000). However, mislocalisations are not equally likely onto each neighbouring finger – localisations are biased towards the middle finger of the hand, with the middle finger being equally mislocalised onto each neighbouring finger (Braun et al., 2011, 2005; Schweizer et al., 2001, 2000, Fig. 1.2).

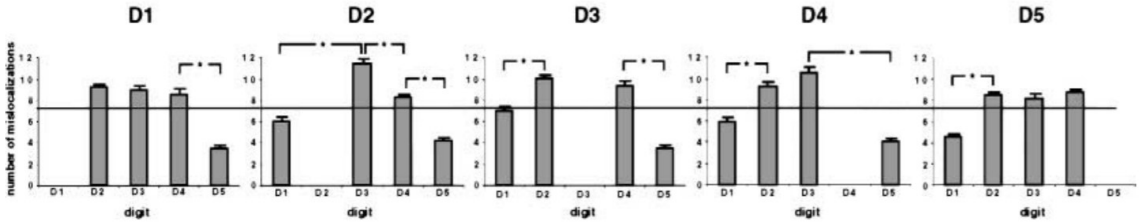

Figure 1.2. Distribution of mislocalisations across the fingers. Label at top of graph indicated stimulated finger, with bars showing the distribution of mislocalisations to the other fingers. Mislocalisations of the fingers are biased towards the middle finger, with mislocalisations on the middle finger being equally likely onto each neighbouring digit. Image source: Schweizer, Braun, Fromm, Wilms, & Birbaumer (2001, p. 438).

This pattern has been well-documented on the fingers, but only one study has investigated tactile localisation of the toes (Cicmil, Meyer, & Stein, 2016). Cicmil and colleagues used the paradigm of most localisation experiments, applying touches to the individual toes and asking participants to identify the stimulated toe. However, unlike previous experiments investigating the fingers, Cicmil and colleagues used a supra-threshold stimulus (a gentle touch from the experimenter's fingertip). Similar to the fingers, they found that mislocalisation biases are more frequent on neighbouring than distant digits (Cicmil et al., 2016). However, they found a marginally different pattern in the direction of mislocalisation biases – the big toe, second toe and middle toe were mislocalised towards the outer toes, whereas the two outer toes were mislocalised towards the big toe (Fig. 1.3). So, significant differences between the hands and feet are only evident in mislocalisation direction of the middle digit. Cicmil et al. suggest that toe mislocalisations arise from a distorted representation of the toes in which each toe is given equal size representation, despite the big toe being much larger than the other toes. This theory may also account for why a symmetrical pattern of mislocalisations is found on the hands, as the fingers are roughly equal in width distribution.

The differences in biases found across the fingers and toes may also reflect their distinct representations in SI, as described above. While the fingers are organised sequentially along the medio-lateral axis in SI (Kolasinski et al., 2016; Martuzzi et al., 2014), the toes, though still ordered sequentially, are possibly ordered along the rostral-caudal axis in the postcentral gyrus (Akselrod et al., 2017). This is similar to the pattern of somatotopic organisation found in monkeys for the hands and feet (Merzenich, Kaas, Sur, & Lin, 1978; Nelson, Sur, Felleman, & Kaas, 1980). Despite these differences between them, the first digits of both the hands (Martuzzi et al., 2014) and feet (Akselrod et al., 2017) similarly share a larger and stronger activation than the remaining digits, suggesting the importance of both of these digits for their specified uses.

Although studies have found that fingers and toes are both somatotopically organised, there is also a large range of variability across participants in the shape, extent and relative positions of representations (Kolasinski et al., 2016). Some studies have shown that there is more overlap than previously thought between neighbouring finger (Besle, Sánchez-Panchuelo, Bowtell, Francis, & Schluppeck, 2014) and toe (Akselrod et al., 2017) representations, which may account for tactile confusions between the neighbouring digits described previously. Specifically, this overlap in representation may be related to the joint use of the fingers (Ejaz, Hamada, & Diedrichsen, 2015). Further studies have investigated how the fingers and toes are represented in congenital one-handers and extreme foot users. When using the foot as you would a hand (i.e. with dextrous individual use of the toes), the toe representations are dispersed into the missing-hand area of the somatosensory cortex (Dempsey-Jones,

Wesselink, Friedman, & Makin, 2019; Hahamy et al., 2017). Moreover, these representations mimic a typical hand representation in that there is greater individuation of the toe representations, greater cortical magnification and therefore enhanced tactile perception of the toes, and the toe representations follow the pattern of somatotopic organisation of the fingers, along the medio-lateral axis of SI (Dempsey-Jones et al., 2019; Hahamy et al., 2017). These findings demonstrate an effect described in healthy participants by Ejaz et al. (2015), that hand use shapes the relative arrangement of finger-specific activity patterns in sensory-motor cortex (Dempsey-Jones et al., 2019).

The studies of tactile localisation presented here for both the fingers and toes have focused only on the pattern of mislocalisations found on the glabrous skin surfaces. In my research I will also investigate the differences in tactile localisation across the hairy skin surfaces of the fingers and toes. I am not aware of any human neurophysiological studies that make specific claims as to whether the hairy skin surface is represented distinctly from the glabrous skin surface in SI, for either the fingers or toes. In primates, however, the hairy skin surface is represented distinctly from the glabrous skin surface in SI, for both the fingers or toes (Merzenich et al., 1978; Nelson et al., 1980). Therefore, we may find that patterns of mislocalisations differ across the two skin surfaces of the fingers and toes, if mislocalisations arise from a distorted representation in SI.

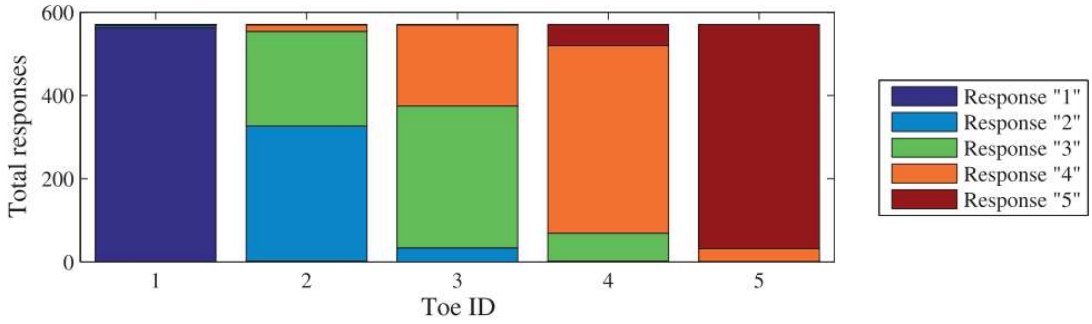

Figure 1.3. Distribution of tactile toe mislocalisations. Identification of the big toe and smallest toe was nearly entirely accurate. Localisation of the middle three toes was accurate around 50% of the time, with mislocalisations being the most common to neighbouring toes. The second and third toe were more frequently mislocalised as smaller toes (towards toe 5), whereas the fourth toe was more frequently mislocalised towards the big toe. Image source: Cicmil, Meyer, & Stein (2016, p. 269).

A similar but different line of research investigates tactile localisation on the palm and dorsum of the hand. This research is distinct from digit localisation as there are no distinct boundaries between points on the continuous skin surface of the hand, as there are between the individual fingers, making it potentially more difficult to distinguish between points. Tactile stimuli are applied to the hand within a 3 x 3 or 4 x 4 grid of equally spaced points, and participants are asked to estimate where they felt the touch, either on the other hand or on an image of the hand. Results have indicated that localisation on the continuous skin surface of the hand is also distorted. On the hand dorsum, points are frequently localised as being more distal than their actual point on the hand (i.e. towards the knuckles [Mancini, Longo, Iannetti, & Haggard, 2011]). This pattern differs on the palm of the hand – smaller and more proximal biases are found on the glabrous skin (i.e. towards the wrist [Mancini et al., 2011]).

Mancini and colleagues also investigated whether stimulation of different afferent fibres alters localisation on the two skin surfaces of the hand, using an infrared laser to selectively stimulate Aβ (innocuous touch), Aδ (pinprick pain), and C fibres (non-painful heat). They found that the pattern of mislocalisations on both the hairy and glabrous skin surfaces did not differ depending on the afferent fibre stimulated (Mancini et al., 2011), suggesting that the direction or magnitude of biases found are not attributable to low-level sensory processing. Instead, they may arise from somatosensory representations of the body (specifically in SI), where the two skin surfaces of the hand have distinct somatotopic representations (in primates, although this is further discussed in the next paragraph; Merzenich, Kaas, Sur, & Lin, 1978; Nelson, Sur, Felleman, & Kaas, 1980). The magnitude of mislocalisation biases likely arise from the size and shape of RFs in SI. RFs for the hairy skin surface of the hand are oval shaped and oriented along the proximo-distal axis of the hand (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961; Brown, Fuchs, & Tapper, 1975), whereas RFs of the glabrous skin are smaller and more rounded (DiCarlo & Johnson, 2002; DiCarlo, Johnson, & Hsiao, 1998). The smaller and more rounded RFs on the glabrous skin result in a more dense representation in SI for the glabrous skin, and therefore there is less error in localisation.

This pattern of tactile mislocalisations has been investigated across the two skin surfaces of the hands, but it has not been investigated across either skin surface of the foot. In my research I will extend the findings of this experiment from the hands to the feet, and therefore provide further information about the origin of these biases. The existing literature examining the somatotopic representations of the feet can allow us to

predict what tactile biases we may find for the feet. Like the hands, the two skin surfaces of the feet have distinct representations in SI (Merzenich et al., 1978; Nelson et al., 1980). Given the substantial conservation of the overall organisation of somatosensory cortex between human and non-human primates (Kaas, 2008), we assume that the separation of the two skin surface representations was conserved between human and non-human primates. As the hairy and glabrous skin surfaces of the foot have distinct representations in SI, we may predict that we would find distinct patterns of mislocalisations across these two skin surfaces, as we did for the hand. Moreover, as the skin surfaces of the foot are also represented separately from the hand in SI (Akselrod et al., 2017), we may find different patterns of results across the two hairy skin surfaces and two glabrous surfaces.

RFs of the two skin surfaces of the feet also appear to be similar (Vedel & Roll, 1982), in contrast to the difference in RF shape and size on the glabrous and hairy skin surface of the hand (Fig. 1.4). RFs for the hairy skin surface of the foot appear to be similar in size, shape and distribution to those found on the hairy skin surface of the hand (Vedel & Roll, 1982). However, for the glabrous skin surface of the foot, Strzalkowski et al. (2018) report that RFs are larger than those on the glabrous skin surface of the hand. Kennedy and Inglis (2002) further specify how specific mechanoreceptor type RFs are distributed in their representations across the glabrous skin of the foot. They describe how all receptors have round to oval shapes (similar to the glabrous skin of the hand), except FA2 receptors, which were large and obscure in dimension, sometimes extending from the glabrous skin onto the hairy skin of the calf (Kennedy & Inglis, 2002; Strzalkowski, Peters, Inglis, & Bent, 2018). Moreover, the

RFs for the toes are smaller than RFs for the heel and middle of the foot (Strzalkowski et al., 2018), reflecting the increased sensitivity of this region. These findings suggest that magnitude of biases found in tactile localisation on the continuous skin surface of the foot may not differ as dramatically between the hairy and glabrous skin as for the hand, given that RFs are larger for the glabrous skin surface of the foot than the hand.

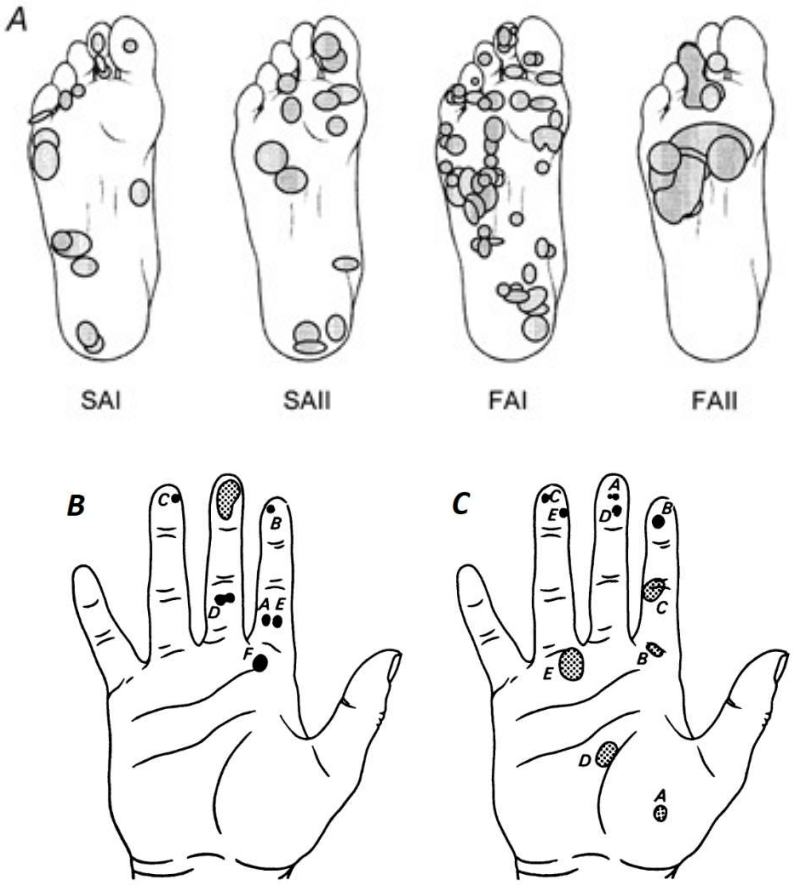

Figure 1.4. RFs on the glabrous skin surfaces of the foot (A) and hand (B and C). (A) shows RFs for SA1, SA2, FA1 and FA2 receptors across the glabrous skin surface of the foot. Most RFs are small and rounded, except FA2 receptors which are more expansive. (B) shows RA (solid black) and PC (dotted) receptors on the glabrous skin of the hand. (C) shows SA1 (solid) and SA2 (dotted) units. All receptor types are small and rounded on the glabrous skin of the hand. Image source (A): Kennedy & Inglis (2002, p. 999). Image source (B and C): Johansson (1978, p. 105).

Another somatosensory function that has been found to be systematically distorted on the hand is tactile size perception. In these studies, two tactile stimuli are applied oriented either along or across the hand, often varying the distance between the two touches. Participants are asked to give an explicit estimate of the distance between the two touches, or asked whether one touch is larger than the other (in a two-alternative forced choice paradigm). On the hand, tactile distances going across the hand are perceived as wider than those going along the hand (Longo & Haggard, 2011), so the hand is perceived as wider than it actually is. Like the consistent pattern of mislocalisations on the hairy skin of the hand, the consistent anisotropies in tactile size perception can also be attributed to the size and shape of RFs for the hairy skin of the hand. Longo and Haggard (2011) suggest in their pixel model that tactile size is simply measured by the number of RFs between the two touched points. RFs are oval-shaped, running along the proximo-distal axis of the hand dorsum, therefore a larger number of RFs are covered by touches going across the hand than along it, resulting in perceived distances being greater across the hand than along it (Longo & Haggard, 2011). This theory is supported by the fact that anisotropies in tactile distance perception are greatly reduced (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015) or non-existent (Green, 1982; Longo & Golubova, 2017; Longo & Haggard, 2011) on the glabrous skin surface of the hand. As RFs are smaller and more rounded on this glabrous skin surface there is less difference in the number of RFs counted when going across or along the hand.

In my research I will investigate tactile size perception across the two skin surfaces of the feet. As described previously, RFs also differ in their size, shape and distribution across the hairy and glabrous skin surfaces of the foot, although not in the

same manner as across the two skin surfaces of the hand. As such, anisotropies in tactile size perception may not vary in the same ways across the two skin surfaces of the feet, as across the two skin surfaces of the hand.

1.2.2.2. The role of higher-order body representations

So far, I have largely discussed the role of the physical structure of the hands and feet and neurophysiological structure of S1 in somatosensory function. However, there is no intrinsic, hard-wired link between a location in a somatosensory map and a body location (Longo, Azañón, & Haggard, 2010), such as is demonstrated by the plasticity of somatosensory maps in congenital one-handers and extreme foot users mentioned previously (Dempsey-Jones et al., 2019; Hahamy et al., 2017). Perceiving the properties of an external object touching the body, such as size or shape, or location on the body, depends on perception of the body itself. This perception of the body itself may be called the body representation, and further differentiated into body schema and body image. As de Vignemont (2010) notes, there has been longstanding confusion and debate about the definitions of these terms. In her investigation of these concepts, she arrives at defining body schema as a cluster of sensorimotor representations that are action-oriented, in which the body is represented as both as the effector and as the goal of the action. Body image seems to include all representations of the body that are not used for action, such as a structural description of the body and relationships between body-parts (visuo-spatial body map) and semantic descriptions of the body (i.e. functional purpose of body parts and categorical relationships between them).

The task of adequately defining these subtypes of body representation is a worthy one – distinguishing between what we refer to as body schema or body image in the literature allows us to more accurately discuss these ideas, and develop theoretical frameworks of body representation. However, as I have mentioned above, there is still debate over the two distinct types of body representation, the body schema and body image. De Vignemont (2010) describes the wide variety of disruptions that occur in representation of the body, positing the question of how to organize the diversity of syndromes that differ on so many levels. Some of these disorders may be described as deficits, such as deafferentation (loss of somatosensory input), or distortions, such as personal neglect (inattention to sensory information). Double dissociations are one way that different subsets of body representation can be distinguished, such as between deafferentation (a disruption of the body schema) and personal neglect (disruption of the body image). However, this is one of the few clear dissociations between syndromes, with many others showing deficits of both body schema and body image (as they are defined above). De Vignemont also presents the argument that the body image may be further categorised as I described in the previous paragraph, in terms of a visuo-spatial body map and semantic descriptions of the body. The few (of many) potential distinctions presented here demonstrate the difficulty in defining body representations – given the wide range of disorders of body representation and possible criteria for differentiating between types of representation, it is easy to disagree over these definitions. De Vignemont and colleagues argue that we should focus less on creating a stark dichotomy between these classifications of body representation (de Vignemont, 2010; Pitron, Alsmith, & de Vignemont, 2018; Pitron & de Vignemont, 2017). In their

co-construction model they suggest that body schema and body image remain two distinct concepts (with respect to their functions), however, these concepts are tightly linked, interacting and reshaping each other in order to minimize prediction error and increase their reliability (Pitron et al., 2018; Pitron & de Vignemont, 2017).

Longo, Azañón and Haggard (2010) also discuss this topic, making the distinction between different types of body representation beyond S1. They describe the construction of perceptions and experiences of somatic objects and events, and of one's own body, as somato*perception*. Somatoperception goes beyond the basic mechanisms of somatosensation, integrating elements such as the current posture of the body (postural schema, sometimes also referred to by the term body schema as discussed above), and the construction and maintenance of a sense of self (conscious body image; Longo et al., 2010). They distinguish this conscious body image further from the type of body image described by de Vignemont (2010) above, as they describe the abstract knowledge of the lexical-semantic knowledge of bodies in general, and configural knowledge of the structure of bodies using the term somato*representation.*

As discussed in the previous paragraphs in relation to the body schema, updating the postural schema relies on a combining afferent and efferent body signals with a stored representation of the body (Longo et al., 2010). Afferent information from mechanoreceptors in the joints, muscles, muscle-tendons, and stretch-sensitive receptors in the skin, and efferent signals from the motor system specifying movements, cannot provide information about the body size, so updating the postural schema must also involve a stored representation of the body containing information about it's structure, i.e. the length and width of respective body parts (Longo et al., 2010). One example of

when this becomes evident is during periods of rapid growth – lack of coordination is frequently seen in children and adolescents when changes in body size occur, as rate of growth exceeds the rate of updating of the stored representation of the body (Hirtz & Starosta, 2002; Visser, Geuze, & Kalverboer, 1998).

A large body of experimental research has also investigated how altering posture also alters our ability to localise touch on the body, looking at crossing the hands (Yamamoto & Kitazawa, 2001), feet (Schicke & Röder, 2006), and fingers (de Haan, Anema, & Dijkerman, 2012). In all these studies crossing the body parts reduces participants' ability to quickly and accurately localise touch on the stimulated body part. This is especially true when the time between stimulation of the crossed body parts is relatively short (anywhere from 100-700ms [de Haan et al., 2012; Schicke & Röder, 2006; Yamamoto & Kitazawa, 2001]). These results suggest that immediately following stimulation, touch is not remapped into external space using the perception of the actual current body posture, but instead using a stored representation of the prototypical or standard posture (de Haan et al., 2012; Longo et al., 2010; Manser-Smith, Romano, Tamè, & Longo, 2020; Romano, Marini, & Maravita, 2017; Romano et al., 2019).

Romano and colleagues (Romano et al., 2017, 2019) went a step further to investigate whether postures of the hand are actually incorporated into our body representations. Using a number of different tasks they showed that the fingers have preferential associations with relative locations in external space. For example, when the thumb is in a relatively lower position than the fingers, and the fingers are in a relatively higher position than the thumb, touches to these digits can be localised faster and with

less error than when they are in the opposite positions (i.e. thumb in a higher position and fingers in a lower position).

They suggest that these associations between the digits and relative positions in external space are incorporated into the representation of these body parts to facilitate tactile localisation. They may arise through evolutionary development, so that our standard posture is similar to how primates grasp during arboreal locomotion (Romano et al., 2019; Schmitt, Zeininger, & Granatosky, 2016). On the other hand, they may arise through ontological development, as early experiences of hand use is physically and functionally constrained so that it induces use of the hands with the thumb in a lower position (Romano et al., 2019). If standard associations between the fingers and external space arise from learning during development, we may expect to find a different pattern of associations for the toes, as they have different anatomical and physical constraints to those of the fingers. However, it is not clear what result we may expect if associations developed through evolution. Although the fingers and toes are serially homologous, and the primate toes are used in a way like their fingers (Rolian, 2009; Szalay & Dagosto, 1988), humans have evolved different uses of the fingers and toes. As such, it is not clear whether the toes would have spatial associations incorporated into their bodily representation, or what it might tell us about the development of associations if they are present.

So far, I have discussed a large amount of research relating to the somatosensory representations of the hands, and some research that indicates the similarities and differences in representations of the feet. But not only are the hands and serially homologous, but the entirety of the limbs (Lewis, 1989). As such, similarities and

differences in the somatosensory representations of the arms and legs may give us further insight into the origins of biases in somatosensation, which may also be informative of the hands and feet. In a study by Stone, Keizer and Dijkerman (2018) they demonstrated the influence of different senses on the body representation of the lower limbs. Specifically when investigating tactile perception of the leg, they used a tactile size estimation task similar to that described above – two stimuli were presented oriented either across or along the thigh or shin, and participants were asked to estimate the distance between the two points (Stone et al., 2018). They showed that participants underestimated the distance between two points going along the shin, specifically, but correctly estimated the distance between two points across the leg. As such, the leg is represented as shorter than it is when using touch alone. Previous research has found the same pattern of underestimation of thigh length compared to width (Green, 1982), as well as the same pattern on the forearm (Green, 1982; Le Cornu-Knight et al., 2014). These similarities in the distortions of tactile perception of the arms and legs suggest that systematic distortions of somatosensation found for these body parts may be a common feature of the limbs, arising from their co-development. As such, we can hypothesise that the co-development of the hands and feet may also result in similarities in the distortion of somatosensory perception between these body parts, despite their physical differences.

Disorders of tactile perception can also give us some insight into the representations of the hands and feet. Finger agnosia is a commonly reported symptom of Gerstmann syndrome, in which individuals experience the selective loss of ability to recognize, identify, distinguish, or indicate individual fingers, on either the patient's

own or another's fingers (Anema et al., 2008; Gerstmann, 1939; Kinsbourne & Warrington, 1962; Mayer et al., 1999). Although finger agnosia is a commonly reported symptom of Gerstmann syndrome, there is evidence to suggest that toe agnosia is a frequently co-occurring symptom, and therefore the symptom should be more inclusively recognised as 'digit agnosia' (Mayer et al., 1999; Rusconi, Pinel, Dehaene, & Kleinschmidt, 2010; Tucha, Steup, Smely, & Lange, 1997). The rate of co-occurrence of finger and toe agnosia suggests that there is a deep functional connection between these two body parts, in particular when it comes to identifying them using the somatosensory body representation. Interestingly, Gerstmann syndrome is usually associated with brain lesions to the left parietal hemisphere and angular gyrus (Anema et al., 2008; Gerstmann, 1939; Rusconi et al., 2010; Tucha et al., 1997), in broadly the same area that neurons encoding body parts exhibited mixed selectivity, i.e. overlapping representations of multiple body parts (Zhang et al., 2017).

Phenomena such as the co-occurrence of finger and toe agnosia, as well as the wealth of research I have described in this introduction that shows the similarities in somatosensory processing for the limbs, leads us to suggest that there may be a single, common representation of these two body parts in higher somatosensory processing. The described similarities may be attributable to similarities in their development through their co-evolution, but research suggests a stronger link between them. One study by Badde, Röder, and Heed (2019) showed how touches on the hand or foot are systematically attributed to the other body part. Participants received two successive, supra-threshold touches on either of the hands or feet, with crossed and uncrossed positions used to distinguish between body-based and external-based representations.

Participants were asked to report which body part received the first touch, although in around 8% of trials they reported that one of the *unstimulated* body parts had received the first touch (Badde et al., 2019). Badde and colleagues report that touch was erroneously attributed to limbs of the same limb type or body side as the correct limb, suggesting that these mislocalisations arise from a high-level representation of the body in which topographic representations are abstracted, and encoded instead in respect to categories such as body type and body side (Badde et al., 2019). This is similar to the high-level representation described by Zhang et al. (2017), however, they specified that body side was not coded in a mixed manner in the posterior parietal cortex. Throughout my thesis I will present further evidence towards common representations of multiple body parts.

In this section I have described the existing literature on how the hands and feet are represented through touch, in both low- and high-level representations. In my research I aimed to extend this knowledge by investigating how representations change across these different body parts, and what this tells us about the origins of somatosensory representations.

1.3. Organisation of the thesis

The aim of this thesis is to contribute to knowledge of somatosensory perception of the hands and feet. In the following chapters I describe research I conducted in my doctoral studies. The main topic of my investigations was how somatosensory representations of the hands and feet compare. I discussed the main motivations for my

work in the previous sections. Here, I summarise the organisation of the thesis in terms of the content of each chapter.

In Chapters 2 I investigate how tactile localisation differs across the hairy and glabrous skin surfaces of the toes. Although tactile localisation has been studied on both the hairy skin of the fingers (Braun et al., 2011; Braun, Ladda, et al., 2005; Schweizer et al., 2001, 2000) and toes (Cicmil et al., 2016), it has not been investigated on the hairy skin surfaces of both these body parts. We know that mechanoreceptor type, distribution and density differs across these body parts, as well as them having distinct and integrated representations in SI and higher cortical areas. The two studies of Chapter 2 aim to investigate at what level tactile mislocalisations occurs, by investigating similarities and shared individual differences across the hairy and glabrous skin surfaces of the hands and feet.

Using the same paradigm as used in Chapter 2, in Chapter 3 I will directly compare individual differences in participants' patterns of mislocalisations across the hands and feet. Although I have discussed the multitude of ways in which the hands and feet differ, in their physical appearance, uses and psychological representations, the fact remains that there are also similarities that likely arise from the co-development of these two body parts. In this study we aimed to investigate whether the similarities between the two body parts are preserved enough to contain any similarities in tactile mislocalisation across the two body parts, despite their overall differences in localisation patterns. The findings of this experiment build on the existing literature that suggests that a common representation of the hands and feet may exist (Badde et al., 2019).

Again in Chapter 4, I use the same paradigm as used in the previous two experiments to investigate whether there are also shared individual differences between the left and right hands. Many of the tactile localisation studies discussed so far tested both the left and right hands, finding no significant differences in tactile localisation across the two hands (Schweizer et al., 2001, 2000; Weinstein, 1962). These nearly identical patterns of tactile localisation across the two hands may simply arise from their bilateral representations in SI (Iwamura, 2000; Iwamura, Iriki, & Tanaka, 1994), or from a common representation of the two hands (Tamè et al., 2011). This study aims to shed more light on the origins of tactile mislocalisations and their commonalities between the two hands.

In Chapter 5 I go on to investigate how tactile localisation differs across the continuous skin surfaces of the hands and feet. Previous research has investigated this across the two skin surfaces of the hand (Mancini et al., 2011), but this has not been investigated on the feet. In this study we wanted to further understand the origin of tactile biases on the two skin surfaces, which have previously been attributed to differences in RFs for the two skin surfaces of the hand (Mancini et al., 2011). RFs on the foot do appear to be similar to those found for the hands (DiCarlo & Johnson, 2002; DiCarlo et al., 1998), although they are little studied. As such, similarities and differences in results found across the hands and feet can be attributable to differences in RFs, or that they are a common feature of the limbs as a whole.

Chapter 6 investigates the differences in tactile size perception, again across both skin surfaces of the hands and feet. Similarly as for Chapter 5, differences in tactile size perception across the two skin surfaces of the hand have been attributed to RF

differences for these two skin surfaces (Longo & Haggard, 2011). This has not been studied on either skin surface of the foot, but again, the similarities or differences in results between the two skin surfaces can shed light on the level at which these distortions occur. This series of studies uses a variety of different methods in order to investigate the true origin of these biases.

In Chapter 7 I use a different approach called double simultaneous stimulation (DSS, Tamè et al., 2011) to investigate the representations of the fingers and toes. In DSS, stimuli are applied to two digits simultaneously, while participants are asked to detect stimuli only on a single target digit. The resulting reaction times (RTs) and error rates show us how touches on multiple digits can occlude touches on other digits, and the relationships between them. This has previously only been studied between the two hands, showing that touches to both the neighbouring finger on the same hand, and what would be the neighbouring finger on the *other* hand, both occlude touches on the target finger. This suggested that there is a single common representation of the two hands. As research has also suggested that there may be a single common representation of the hand and foot, if DSS was used on the digits of the hand and foot we may find a similar occlusion effect. We investigated whether this occurred for the hairy skin surface of the fingers and toes.

Chapter 8 went further into somatosensory representations of the body to manipulate posture and the way that this alters the representations of the body. In previous studies, Romano and colleagues (Romano et al., 2017, 2019) showed that the fingers had specific postures that facilitated the localisation of touch – when the thumb was in a relative bottom position and the fingers relative top. They suggested that these

postures were learned throughout development, and therefore through experience we learned that canonical postures like this are frequent enough to facilitate tactile localisation when in them. In this study we investigated whether the toes also have canonical postures. We did this by using the paradigm adapted from Romano and colleagues. Similarities in the canonical postures held by the hands and feet could indicate that they develop much deeper through evolution to be a general characteristic of the limbs. As the uses of the hands and feet differ greatly now, similarities in their usage would likely not originate simply from development and experience. On the other hand, differences between the fingers and toes may indicate that these canonical postures are learned from use and experience.

Finally, I summarise my findings in Chapter 9. I discuss how the similarities and differences in somatosensory representations of the hands and feet informs our understanding of how distortions in these representations arise, and how they are organised for varying task requirements. I also discuss the limitations of my study and possible directions for future research.

Chapter 2: Tactile confusions of the fingers and toes

2.1. Introduction

The ability to localise tactile stimuli on the skin is a fundamental function of the somatosensory system. Nevertheless, research has shown that there are systematic biases in this ability. For example, on the hand dorsum, consistent distal (i.e., towards the knuckles) and radial (i.e., towards the thumb) biases in localisation have been found (Culver, 1970; Mancini et al., 2011). However, a distinct pattern of biases is found when identifying which of the individual fingers was touched, as opposed to localising touch on the continuous skin surface. When using a tactile stimulus near to the sensory threshold, finger mislocalisations on the glabrous skin are biased more towards neighbouring fingers than distant fingers (Braun, Ladda, et al., 2005; Schweizer et al., 2001, 2000). Moreover, mislocalisations are not equally likely onto each neighbouring finger, but more common towards the middle and ring fingers than the outer fingers (Braun et al., 2011; Braun, Ladda, et al., 2005; Schweizer et al., 2001; Tamè, Wühle, Petri, Pavani, & Braun, 2017). It is unsurprising that differences occur in mislocalisation across the continuous skin surface of the hand versus the individual fingers – localising touch to an individual finger may be simpler than localising a point of touch on the palm or dorsum of the hand as the fingers provide an inherent structure and categorical decision, as opposed to the potentially infinite possibilities on the continuous skin. Further to this, the fingers are represented separately both from one another (Besle et al., 2014; Martuzzi et al., 2014), and from the rest of the hand (Gálvez-García, De Haan, Lupiañez, & Dijkerman, 2012; Haggard, Kitadono, Press, & Taylor-Clarke, 2006). This

is evident in body representation disturbances such as finger agnosia, a symptom of Gerstmann syndrome in which individuals experience the selective loss of ability to recognise, identify, distinguish or indicate individual fingers, on either the patient's own or another's fingers (Anema et al., 2008; Gerstmann, 1939; Kinsbourne & Warrington, 1962; Mayer et al., 1999). Even in healthy adults, identifying touch to an individual finger is not as straightforward as one might expect (Rusconi et al., 2014; Rusconi, Gonzaga, Adriani, Braun, & Haggard, 2009; Tamè, Dransfield, Quettier, & Longo, 2017).

Not only does the pattern of mislocalisations differ between the individual fingers and the continuous skin surface of the hand, it appears to differ between the hairy and glabrous skin surfaces as well. Distal and radial biases are found in localising points on the hand dorsum, but no overall biases are found when localising points on the palm of the hand (Mancini et al., 2011). The difference in strength of bias on the two skin surfaces of the hand may be attributable to increased sensitivity on the palm (Ackerley et al., 2014; Johansson & Vallbo, 1979), however, the direction of biases on the hand dorsum are consistent across tactile (Aβ), thermal (C), and painful (Aδ) fibers, indicating it is unlikely that directional differences in biases arise during low-level processing of different afferent pathways (Mancini et al., 2011). Instead, they likely arise from separate somatotopic maps of the palm and dorsum in the somatosensory cortex. Single cell recordings in old world and owl monkeys show that the somatotopic map in the postcentral parietal cortex is not represented as a continuous, 3-D homunculus, but is represented as separate somatotopic maps of each skin surface (Merzenich et al., 1978; Nelson et al., 1980). Given the substantial conservation of the

overall organisation of somatosensory cortex between human and non-human primates (Kaas, 2008), we assume that the separation of the two skin surface representations was conserved between human and non-human primates. As such, it is likely that differences in the pattern of mislocalisations across the two skin surfaces arises from processing in the primary somatosensory cortex (S1), but may also involve higher-level processing in parietal areas posterior to S1 (Longo et al., 2010). However, higher-level processing in parietal areas posterior to S1 may also be involved (Longo et al., 2010) – similarities in the observed biases on the two skin surfaces indicate that biases may also occur at a higher level, where the body is represented as a 3-D, volumetric object, as opposed to separate 2-D skin surfaces (Longo, 2014).

As the hands and feet are serially homologous structures that co-evolved in human evolution (Rolian et al., 2010), there are many common physical characteristics of the hand and foot, such as the presence of hairy and glabrous skin surfaces (Marieb, 2012). A number of idiosyncrasies in the mental representation of these physical properties also appear to be common to both the hand and the foot. For example, there is evidence that toe agnosia also commonly occurs in Gerstmann syndrome alongside finger agnosia, suggesting that beyond the physical similarities in structure, there is a deeper level of similarity in how the digits are represented in relation to the rest of the hand or foot (Mayer et al., 1999; Tucha et al., 1997). Moreover, both the hairy and glabrous skin surfaces of the hands and feet have separate somatotopic maps in owl monkeys (Merzenich et al., 1978). However, there is evidence that processes such as tactile localisation do differ across the hands and feet. For example, tactile localisation of the toes is less precise than on the fingers, especially for the second, third and fourth

toes (Cicmil et al., 2016; Halnan & Wright, 1960). This may be a result of differences in size and shape of the bones present in both the hands and feet (Rolian et al., 2010; Marieb, 2012), differences in the way the fingers and toes are ordered in the somatosensory cortex (Akselrod et al., 2017; Martuzzi et al., 2014), or differences in usage, as in humans the toes are not used independently and dextrously as the fingers are, though with the intriguing exception of compensatory use of the feet in congenital one-handers (Hahamy et al., 2017). Differences in mechanoreceptor density and activity may also affect the ability to localise tactile stimuli – for example, mechanoreceptors have much higher activation thresholds on the glabrous skin of the foot than the hand, which may reduce ability to precisely localise touch (Kennedy & Inglis, 2002; Rolian et al., 2010).

One recent study reported a consistent pattern of mislocalisations for stimuli on the glabrous skin of the toes (Cicmil et al., 2016). Cicmil and colleagues measured this using a simple task: the experimenter stimulated a toe on each trial, using a suprathreshold stimuli, and asked the participant to identify the toe. As for the fingers, touches on the glabrous skin of the toes were more frequently localised to neighbouring toes than distant toes. Performance was worst for the middle three toes, where incorrect localisations were not equally likely to either neighbouring toe but biased towards one of their neighbours. The second and third toe were more frequently localised towards the outer toes, whereas the fourth toe was more frequently localised towards the big toe. It is possible that these biases arise from processing in S1 such as the results of Mancini et al. (2011). However, Cicmil and colleagues describe these biases as arising from an inaccurate internal body representation used when remapping somatosensory

information onto the body in external space. Particularly, they suggest that their results reflect an "equal spatial representation hypothesis" wherein toes are represented as being of equal size, despite their actual size differences. This hypothesis accounts for the directional bias observed for each toe, including the mostly veridical identification of the big toe and small toe, as the perceived location in the body representation and actual location in external space are misaligned most significantly for the middle three toes.

Other studies support the hypothesis that tactile localisation occurs in primary somatosensory cortex and higher cortical areas. Localising touch on the body should be seen as a two-step process – first, touch is localised on the somatotopic map, then second, the somatotopic location is mapped onto the body representation (Longo et al., 2010). There is evidence that tactile biases occur in early somatosensory processing (when touch is localised on the somatotopic map), from differences in tactile biases across the two skin surfaces of the hand (Mancini et al., 2011), which are represented separately in the somatosensory cortex of old world and owl monkeys (Merzenich et al., 1978; Nelson et al., 1980). As well as the hand dorsum and palm being represented separately, so are the two surfaces of the fingers (Nelson et al., 1980). In contrast, behavioural studies in humans have found that the conscious body image represents the hands as complete, volumetric units (Longo, 2014). Such differences suggest that different processing stages represent the body either in terms of a collection of 2-D skin sheets (e.g., somatotopic maps) or as a coherent 3-D object (e.g., the body image) (Longo, 2015). If biases in tactile localisation arise in early somatosensory processing, using distinct hairy and glabrous skin representations in the somatosensory cortex, there may be a distinct pattern of mislocalisations for each skin surface of the fingers. In

contrast, if biases arise in higher-level processing involving the three-dimensional representation of the fingers, the same pattern of mislocalisation across the fingers could be expected on both the hairy and glabrous skin. In the present study we therefore compared patterns of mislocalisation of touch on both the glabrous and hairy skin surfaces of the toes (Experiment 1) and the fingers (Experiment 2).

2.2. Experiment 1

This study aims to investigate whether tactile mislocalisation of touch to the toes arises from early somatosensory maps or from higher-level body representations. By using a method closely modelled on the study of Cicmil et al. (2016), we aimed to: (1) replicate the pattern of results they found on the glabrous surface of the toes; (2) investigate whether the same pattern of results is found on the hairy surface of the toes; and (3) determine whether individual differences in patterns of mislocalisation are shared across the two surfaces.

2.2.1. Methods

Participants

Twenty individuals participated (10 female; mean age = 30 years; range = 19 – 58). Participants all reported normal or corrected-to-normal vision and normal touch. Eighteen participants were right-handed and two left-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean = 63, range = -92 – 100). The same 18 participants were right-foot dominant, and two left-foot dominant as assessed by the Waterloo Footedness Questionnaire (Elias, Bryden, & Bulman-Fleming, 1998;

mean = 44, range = -40 – 100). EHI and WFQ scores were strongly correlated across participants ($r = 0.74$, $p < 0.001$). All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

The mislocalisations reported by Cicmil et al. (2016) were strikingly strong. The directionality indices (DIs) for toes 2 and 3 (which are the two most characteristic mislocalisations reported) showed Cohen's *d*'s of 1.81 and 1.04, respectively. We conducted a power analysis using G*Power 3.1 (Faul, Erdfelder, Buchner, & Lang, 2007) taking the smaller of these two effect sizes, an alpha value of 0.05 and power of 0.95, which indicated that 12 participants were required. Thus, with 20 participants our experiment has appropriate statistical power to replicate the results of Cicmil and colleagues and to extend their results to the top of the toes.

Apparatus and stimuli

The experimental setup is shown in Figure 2.1. Participants were asked to sit with their leg outstretched and bare foot resting on a stool (height: 40cm), with toes pointing upwards so that both the top and bottom surfaces of the foot were easily accessible to the experimenter. A piece of black cardboard attached to a post was used as a partition to occlude the participant's sight of their toes. Information about the current trial was presented to the experimenter on a monitor by a custom MATLAB script (Mathworks, Natick, MA), but was not visible to the participant. Participants gave their responses verbally, which were manually entered into MATLAB by the experimenter.

Figure 2.1. Experimental set-up for Experiment 1. Participants sat on a chair with their left foot resting on a stool, giving the experimenter access to both sides of the toes. A black cardboard partition was used to occlude participant's sight of their toes.

Procedure

On arriving to complete the experiment, participants were evaluated on their hand and foot dominance using the Edinburgh Handedness Inventory and the Waterloo Footedness Questionnaire.

The procedures were closely modelled on those used by Cicmil and colleagues (2016). Cicmil and colleagues reported that while the pattern of bias was consistent across the dominant and non-dominant foot, biases were stronger on the non-dominant foot. As we expected the majority of participants to be right-foot dominant, we chose to test all participants on their left foot, regardless of assessed foot dominance, for

consistency. Once participants were seated with their foot in a comfortable position on the stool, they were instructed to fixate on a yellow sticker on the partition to keep their gaze position constant (Medina, Tamè, & Longo, 2018). They were also instructed to keep their feet as still as possible throughout each experimental block. The experimenter used the tip of her finger to apply tactile stimulation to the section of the participant's toe between the metatarsophalangeal joint (at the base of the toe) and the interphalangeal joint (in the middle of the toe), for around 500 ms. Stimulation was well above detection threshold (estimated 15 to 20 g of force), but indentation of the skin was the only visible motion caused by the stimulation. One toe was stimulated per trial. Participants were asked to respond as quickly and accurately as possible, by verbally identifying which toe they felt had been stimulated. Toes were identified by numbers from 1 to 5: the big toe corresponded to number 1, through to the little toe which corresponded to number 5. Participants generally responded within 1 to 3 seconds after stimulation, so that overall stimulation was applied at a rate of roughly 20 trials per minute. Individual response times were not recorded.

There were four experimental blocks, two in which the hairy skin of the toes was stimulated and two in which the glabrous skin of the toes was stimulated. ABBA counterbalancing was used to vary order of presentation, with the first condition counterbalanced across participants. Each block contained 125 trials, 25 for each of the 5 toes. Each surface of each toe was therefore stimulated a total of 50 times. The order of digit stimulation was pseudo-randomised within each block of trials, so that there was an approximately equal number of each type of preceding trial. Between each block, participants were allowed a short break.

Data Analysis

Our main analyses closely followed those of Cicmil and colleagues (2016). A directionality index (DI) was calculated in order to give a single value to indicate both direction and magnitude of bias in toe selection. For each toe, the mean of the responses given to identify which toe was stimulated was calculated, minus the actual digit number of the stimulated toe:

DI = (mean of response toe numbers - stimulated toe number)

A positive DI indicates a lateral bias (towards toe 5), with greater values indicating stronger bias i.e. if the participant responded toe 5 was stimulated when it was toe 3, DI = 5 – 3 = 2. A negative DI indicates a medial bias (towards toe 1), again where greater values indicate stronger bias, i.e. response of toe 2 when toe 3 stimulated, DI = 2 – 3 = -1. DI scores of zero indicate no directional bias in responding, but may occur in two different scenarios. Firstly, if responses to stimulation of toe 3 were entirely accurate, i.e. DI = 3 – 3 = 0. Secondly, if participants had responded equally to neighbouring toes (2 and 4), i.e. DI = 3 – 3 = 0. As such accuracy was also used as a measure of performance on the task.

Where we found important null results we carried out Bayesian statistical tests in order to assess whether the null hypothesis (H_0) should be accepted over the alternative hypothesis (H_1). In these cases, we reported BF_{01}, which expresses the likelihood of H_0 relative to H_1 given the current data. Bayesian repeated-measures ANOVAs were conducted using JASP 0.8.2.0 (Wetzels, Grasman, & Wagenmakers, 2012).

2.2.2. Results and discussion

Accuracy and directional biases

Figure 2.2 shows confusion matrices for tactile toe localization on the glabrous skin of the bottom of the toes (left panel) and the hairy skin of the top of the toes (right panel). The pattern on the glabrous skin was very similar to that reported by Cicmil and colleagues (2016). Localisation accuracy was highest for toes 1 and 5 (0.98 and 0.89 respectively), but poorer for toes 2, 3, and 4, where the majority of mislocalisations were made onto neighbouring toes (see Figure 2.3, right panel). This pattern replicates the findings of Cicmil and colleagues, as does our finding that middle toe identification errors were not random but biased towards the lateral toes for toes 2 and 3. The left panel of Figure 2.3 shows DI values. DI values were significantly different from zero for toe 2 (*M*: 0.37, SD: 0.30), $t(19) = 5.45$, $p < 0.001$, $d = 1.23$, and toe 3 (*M*: 0.18, SD: 0.17), $t(19) = 3.18$, $p < 0.01$, $d = 1.06$, indicating a bias towards the lateral side of the foot. For toe 4, in contrast, there was a significant medial bias (*M*: -0.19, SD: 0.17), $t(19) = -4.84$, $p < 0.001$, $d = 1.12$. These results provide a direct replication of the main findings of Cicmil et al. (2016) that there are consistent directional biases for tactile toe localization in response to stimulation of the bottom of the toes.

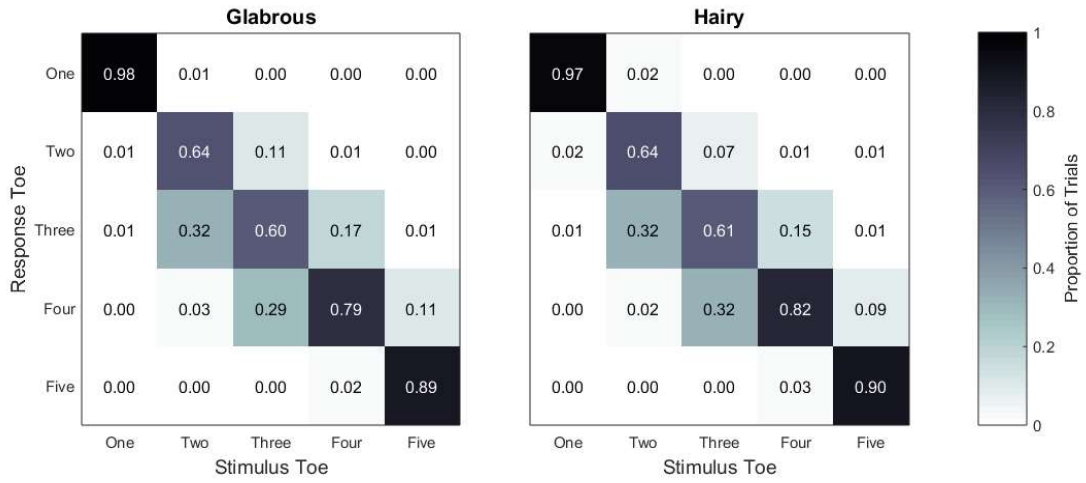

Figure 2.2. Confusion matrices from Experiment 1 showing the proportion of stimuli judged as located on each of the five toes as a function of which toe was actually stimulated. Toes were identified by numbers one (the big toe) through five (the small toe). Data from the glabrous skin of the bottom of the toes is shown in the left panel and data from the hairy skin of the top of the toes is shown on the right panel. The proportion of correct responses for each toe is shown along the diagonal from the top-left to the bottom-right. By definition, each column adds up to exactly 1. Highly similar patterns of mislocalisations were observed for the two sides of the toes.

The novel question in this study was whether similar results would also be found for the hairy skin on the top of the toes. As can be seen in Figure 2.2, the confusion matrices on the two sides of the foot were extremely similar. As on the glabrous surface, localization accuracy on the hairy surface of the toes was highest for toes 1 and 5 (0.97 and 0.90 respectively), but poorer for toes 2, 3, and 4. DI values indicated significant lateral biases for the tops of toe 2 (*M*: 0.35, SD: 0.24), $t(19) = 6.46$, $p < 0.001$, $d = 1.46$, and toe 3 (*M*: 0.24, SD: 0.22), $t(19) = 4.83$, $p < 0.001$, $d = 1.09$, but a significant medial bias for toe 4 (*M*: -0.13, SD: 0.26), $t(19) = -3.79$, $p < 0.01$, $d = 0.87$ (Figure 2.3, left panel). To directly compare the similarity of the pattern of mislocalisations on the two surfaces of the toes, we calculated the correlation between the two grand average response matrices (as shown in Figure 2.2), excluding the diagonals (i.e., the correct

responses). This correlation was essentially perfect, $r(18) = 0.99$, $p < 0.01$, showing that the overall mislocalisation pattern was highly similar on the two sides of the foot. Thus, these results show that the pattern of mislocalisations which Cicmil and colleagues reported following stimulation of the glabrous skin of the bottom of the toes appears in a very similar way following stimulation of the hairy skin of the tops of the toes.

To further investigate the similarities of performance on both skin surfaces of each toe, repeated-measures ANOVAs were performed with two factors: Stimulated Toe (1 to 5) and Skin Surface (hairy/glabrous). DI and accuracy were tested separately as dependent variables. The results of the first ANOVA showed that performance was significantly different across the toes ($F(4,76) = 36.17$, $p < 0.01$, $\eta_p^2 = 0.66$). Post-hoc comparisons confirmed that all toes were significantly different from each other, apart from toes 4 and 5 (all $p < 0.05$, Bonferroni corrected for multiple comparisons). As shown in the left panel of Figure 2.3, while toes 4 and 5 show comparable medial bias, lateral bias for toe 2 was significantly stronger than for toe 3. This is consistent with Cicmil and colleagues' equal spatial representation hypothesis (toes are represented of being of equal size, despite differing in actual size), in which toes 2 and 3 are the most displaced from their actual spatial location. The ANOVA also confirmed that DI was not significantly different between the two skin surfaces of the foot ($F(1,19) = 0.76$, $p > 0.05$, $\eta_p^2 = 0.04$), and there was no difference in DI of each toe depending on which skin surface was stimulated ($F(4,76) = 1.48$, $p > 0.05$, $\eta_p^2 = 0.07$). A Bayesian repeated-measures ANOVA provided moderate evidence in support of the null hypothesis, that there was no difference in DI on the two skin surfaces ($BF_{01} = 5.70$), and strong evidence against there being an interaction of toe and surface ($BF_{01} = 13.48$).

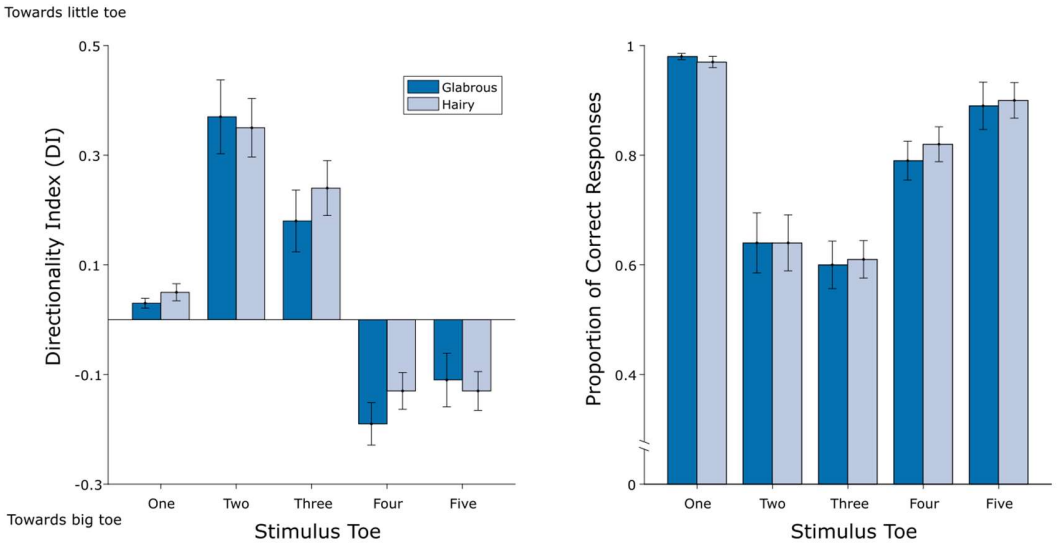

Figure 2.3. Results from Experiment 1. The left panel shows the grand average DI scores for each toe, on the glabrous skin on the bottom of the foot, and hairy skin on the top. The right panel shows the grand average percentage of correct responses made to each toe, on the glabrous skin on the bottom of the foot, and hairy skin on the top. Toes were identified by numbers one (the big toe) through five (the small toe). Error bars represent the standard error of the mean. Highly similar patterns of results were found for the two sides of the toes for both DI and accuracy.

The second ANOVA again indicated that accuracy was significantly different depending on which toe was stimulated ($F(4, 76) = 27.59$, $p < 0.01$, $\eta_p^2 = 0.59$), with post-hoc comparisons revealing that all toes apart from toes 2 and 3 showed significant differences in accuracy of responses (see right panel of Figure 2.3). This finding again lends itself to Cicmil and colleagues' equal spatial representation hypothesis. The ANOVA also confirmed that overall accuracy was also not different depending on which skin surface was stimulated ($F(1,19) = 0.35$, $p > 0.05$, $\eta_p^2 = 0.02$), and did not differ depending on which surface of each toe was stimulated ($F(4,76) = 0.32$, $p > 0.05$, $\eta_p^2 = 0.02$). A Bayesian repeated-measures ANOVA provided moderate evidence in support of the null hypothesis that there was no difference in accuracy on the two skin

surfaces (BF_{01} = 6.40), and strong evidence that there were no differences in accuracy for each toe, depending on which skin surface was stimulated (BF_{01} = 20.15).

Shared individual differences across the two sides of the toes

If the patterns of mislocalisation we have described arise from higher-level body representations in which the different skin surfaces of the toes are integrated into a volumetric, 3-D representation of the whole toe, then person-to-person differences in the pattern of mislocalisation should be shared across the two surfaces. The results above show that there are highly similar patterns of mislocalisations on the two surfaces of the toes at the level of grand averages. We also investigated whether idiosyncratic differences across participants are also common to the two sides of the toes. To isolate individual differences in each participant we used a *leave-one-participant-out* procedure in which we regressed the 20 off-diagonal cells (i.e., the localisation errors) of each participant's confusion matrix on the grand average confusion matrix for the other 19 participants. The resulting residuals quantify the way in which a given participant's confusion matrix differs idiosyncratically from the pattern shown by the other participants. Critically, this procedure eliminates differences between participants in overall levels of accuracy, isolating the *pattern* of confusions between fingers, rather than overall performance. For example, two individuals may produce the same DI for toe 5 (their overall performance), but have different *patterns* of performance. Such as if the first person continually identified toe 5 as toe 3, whereas the second person responded an equal number of times that toe 5 it was toe 2, 3 or 4. In these two cases, the first person would show a relatively strong bias for toe 3, and weak biases for toes 2

and 4, whereas the second person would show moderate biases for toes 2, 3 and 4. Moreover, individuals may even show biases in the opposite direction to those reported in the analysis of overall bias. These residuals were calculated separately for the confusion matrices on the top and bottom of the toes, resulting in two sets of residuals per participant.

If there are shared individual differences on the two sides of the toes, the two sets of residuals for a given participant should be similar. That is, a participant who differs idiosyncratically from other people on the bottom of the toes should also differ in the same way on the top of the toes. For example, if a person showed strong biases for toe 3, but weak biases for toes 2 and 4 on both skin surfaces, this may reflect idiosyncratic differences in performance. In contrast, if a person showed strong biases for toe 3 and weak biases for toes 2 and 4 on the glabrous skin, but moderate biases for toes 2, 3 and 4 on the hairy skin (same DI, different pattern of results), this may reflect that there are not idiosyncratic differences in performance. To assess this, we used a cross-correlation classification procedure. For each participant, we calculated the correlation between the two patterns of residuals, the within-participant cross-correlation. Then we calculated the 38 cross-correlations comparing each of that participant's two patterns to the opposite pattern of each of the other 19 participants. Classification accuracy was calculated for each participant as the percentage of those 38 between-participant correlations which were smaller than the within-participant cross-correlation.

On average, classification accuracy was 82.37%, significantly higher than chance (i.e., 50%), $t(19) = 7.89$, $p < 0.001$, $d = 1.76$. Across participants, classification

accuracy ranged from 18.42% to 97.37%, but exceeded 50% in 19 of 20 participants. This provides strong evidence for shared individual differences in mislocalisation patterns on the two surfaces of the toes. Although the pattern of mislocalisations appears to be highly consistent across participants, as shown by Cicmil et al. and the current replication, there are nevertheless idiosyncratic differences between people in mislocalisations, that are consistent across the two skin surfaces. This adds support to our novel finding that participants show consistent patterns in mislocalisation across the two skin surfaces at the group level.

These results replicate the highly stereotyped pattern of mislocalisations found by Cicmil et al. (2016) on the toes, and showed that similar patterns of mislocalisation are found on both the hairy and glabrous skin. Moreover, we showed that although the pattern is highly consistent across participants, there are individual differences in task performance that are consistent across the two skin surfaces. This result indicates that mislocalisations arise at a level of somatosensory processing in which the toes are represented as complete, volumetric units, and supported that directional disturbances in localisation arise from higher-order representations of the body.

Effect of previously stimulated toe on current toe identification

To fully replicate the analyses carried out by Cicmil and colleagues, we investigated the effect of identity of the previously stimulated toe on the directionality of identification errors. Cicmil and colleagues investigated this for toes 2 and 3, as responses to these toes were significantly biased in their analysis. As responses to toe 4 also showed significant biases in our analysis, we included it our analyses. Toes 1 and 5

were compared in the analysis as 'previously stimulated toes', as accuracy rates for these toes were high and they are separated by the greatest distance (Cicmil et al., 2016). Response data for the two surfaces of the foot was grouped according to which toe had been stimulated on the immediately preceding trial and DI and accuracy were calculated.

On both skin surfaces, when toe 1 was immediately preceding, mean DI values for toes 2 (hairy: 0.19, glabrous: 0.16) and 3 (hairy: 0.03, glabrous: 0.08) were close to zero, indicating little directional bias in responding. DI score for toe 4 was greater than in the original analysis on both skin surfaces when preceded by toe 1 (hairy: -0.21, glabrous: -0.42), indicating a stronger bias towards toe 1. When toe 5 was immediately preceding, mean DI values for toes 2 (hairy: 0.37, glabrous: 0.42) and 3 (hairy: 0.38, glabrous: 0.24) were greater than in our original analysis, indicating a stronger bias towards toe 5. DI score for toe 4 were closer to zero then in our original analysis when preceded by toe 5 (hairy: -0.14, glabrous: -0.27), indicating little bias in responding. Our findings replicate those reported by Cicmil and colleagues, showing that identification of the current toe is biased in the direction of the immediately preceding toe. DI was significantly different depending on whether toe 1 or toe 5 was previously stimulated, on both surfaces of the second toe (paired t-tests, glabrous: $t(19) = -3.30$, $p < .01$, $d = 1.27$; hairy: $t(19) = -3.17$, $p < .01$, $d = 0.70$), and the hairy skin of the third toe (paired t-test, $t(19) = -5.52$, $p < .01$, $d = 1.23$).

Error rates also differed depending on which toe was stimulated on the immediately preceding trial. On both skin surfaces, error rates were greatest for toe 2 following stimulation of toe 4, and for toes 3 and 4 following toe 5. This corroborated

the findings of Cicmil and colleagues, that error rate increases the further the currently stimulated toe is from the preceding toe. Number of errors was significantly different depending on whether toe 1 or 5 was previously stimulated for the glabrous skin of the second toe (paired t-test, $t(19) = 2.95$, $p < 0.01$, $d = 0.75$) and hairy skin of the third toe (paired t-test, $t(19) = 3.21$, $p < .01$, $d = 0.89$).

In addition to the analyses carried out by Cicmil and colleagues, we investigated whether DI was significantly different on the two skin surfaces of each toe, depending on the previously stimulated toe. Repeated-measures ANOVAs were performed with two factors: Previously Stimulated Toe (1 to 5) and Skin Surface (hairy/glabrous). Each of the currently stimulated toes (2, 3 and 4) were tested separately as dependent variables. Each toe showed a significant effect of Previously Stimulated Toe, (toe 2: $F(4, 76) = 10.06$, $p < 0.001$, $\eta_p^2 = 0.72$, toe 3: $F(4, 76) = 13.40$, $p < 0.001$, $\eta_p^2 = 0.77$, toe 4: $F(4, 76) = 3.22$, $p = 0.04$, $\eta_p^2 = 0.45$), showing again that previously stimulated toe biases current toe identification. For two of the toes there was no significant effect of Skin Surface, (toe 2: $F(1, 19) = 0.56$, $p = 0.82$, $\eta_p^2 = 0.003$, toe 3: $F(1, 19) = 0.32$, $p = 0.58$, $\eta_p^2 = 0.02$), indicating DI was not significantly different on the hairy and glabrous skin. However, there was a significant effect of Skin Surface for toe 4 ($F(1, 19) = 11.79$, $p < 0.01$, $\eta_p^2 = 0.38$). There was a trend for stronger bias towards toe 5 on the glabrous skin than on the hairy skin, although post-hoc comparisons showed that strength of bias was only significantly different on the two skin surfaces when the immediately preceding stimulation was to the big toe, $t(19) = 2.87$, $p = 0.01$, $d = 0.70$. None of the three interactions were significant (toe 2: $F(4, 76) = 92$, $p = 0.46$, $\eta_p^2 = 0.05$, toe 3: $F(4, 76) = 2.09$, $p = 0.09$, $\eta_p^2 = 0.10$, toe 4: $F(4, 76) = 2.31$, $p = 0.07$, $\eta_p^2 = 0.11$). This

supports the findings of our original analysis, that the characteristic pattern of mislocalisations of the toes is consistent across the hairy and glabrous skin surfaces.

2.3. Experiment 2

In the second experiment, we used the same method (adapted for the hands) to investigate whether the pattern on the toes is congruent with localisation on the hairy and glabrous surface of the fingers.

2.3.1. Methods

Subjects

Twenty participants took part in the experiment (11 female; mean age = 30 years; range = 18-46). Participants all reported normal or corrected-to-normal vision and normal touch. Eighteen participants were right-handed and two left-handed, as assessed by the Edinburgh Handedness Inventory (mean = 55 years, range = -83 – 100). The same 18 participants were right-foot dominant, and two left-foot dominant as assessed by the Waterloo Footedness Questionnaire (mean = 43, range = -20 – 100). EHI and WFQ scores were strongly correlated across participants ($r = 0.70$, $p < 0.001$). All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

Procedure

The protocol was kept as close to Experiment 1 as possible, although we altered our method of applying the stimuli to avoid problems such as were encountered by

Cicmil et al. (2016). In their experiment, the same strength stimuli were used across the fingers and toes, resulting in ceiling effects in localisation of the fingers (i.e., literally no mislocalisations were reported on the fingers for any of their participants). As the fingers have a small point localisation threshold and pressure sensitivity threshold in comparison to the toes a near-threshold stimulus is needed to give a clear pattern of mislocalisations (Schweizer et al., 2000). Therefore, stimulation was applied using von Frey hairs. This allowed the experimenter to present weaker and more precise force to the fingers than manual stimulation. The strength of von Frey hair used was determined at the beginning of the experiment by finding the threshold stimuli for each participant where they scored roughly 70% correct across all fingers. Threshold testing was done separately for both sides of the hand, although the most frequently used strength was the same for both skin surfaces (mean strength glabrous = 2.30g, range = 1.65g – 2.83g; mean strength hairy = 2.28g, range = 1.65g – 2.83g). Tactile stimulation was applied to the medial phalanx of the finger or proximal phalanx of the thumb for on average 500ms.

Participants were always tested on the left hand to remain consistent with Experiment 1, where the left foot was tested. Participants sat on a chair with their arm resting on a desk. The hand was kept in a neutral posture, with the fingers slightly apart. The hand was either flat with the palm against the desk or with the back of the hand against the desk, depending on the condition. Participants wore an eye mask to prevent vision of their hand. Fingers were identified by numbers from 1 to 5: the thumb corresponded to number 1, through to the little finger which corresponded to number 5.

2.3.2. Results and Discussion

Accuracy and directional biases

Confusion matrices for Experiment 2 are shown in Figure 2.4. The left panel of Figure 2.4 shows the proportion of correct localisations were again highest for the thumb than for other fingers on the glabrous skin of the hand (0.89). In contrast to the findings on the toes, the little finger had the least correct localisations (0.52). Tactile identification was again less accurate for the index, middle and ring finger with accuracy decreasing from the index to the ring finger. As for the toes, finger identification errors were not random but biased towards the little finger for the index finger (*M*: 0.20, SD: 0.17), $t(19) = 5.27$, $p < 0.001$, $d = 1.18$, and towards the thumb for the ring finger (*M*: -0.40, SD: 0.24), $t(19) = -7.44$, $p < 0.001$, $d = 1.67$. In contrast to the toes, however, there was no selection bias for the middle finger on either skin surface, suggesting that lateral or medial fingers were chosen interchangeably (*M*: -0.04, SD: 0.01), $t(19) = -1.77$, $p > 0.05$, $d = -0.40$.

The right panel of Figure 2.4 shows the results from the hairy skin of the back of the fingers. Consistent with the glabrous skin of the hand, finger identification decreased in accuracy from the thumb (0.77) to the little finger (0.51). The bias in identification errors for the hairy skin was consistent from the glabrous skin, as opposed to those on the hairy skin of the feet. DI values were biased towards the little finger for the index finger ($t(19) = 7.82$, $p < 0.001$, $d = 1.82$) and towards the thumb for the ring finger ($t(19) = -7.47$, $p < 0.01$, $d = -1.63$). Again, there was no significant bias for the middle finger ($t(19) = 0.98$, $p > 0.05$, $d = 0.22$). To directly compare similarity of participants' performance on the two surfaces of the hands, the grand average responses to

stimulation on the top and bottom of the hand (see Figure 2.4) were again correlated. Biases in mislocalisation were highly consistent across the two surfaces ($r = 0.82$, $p < 0.01$).

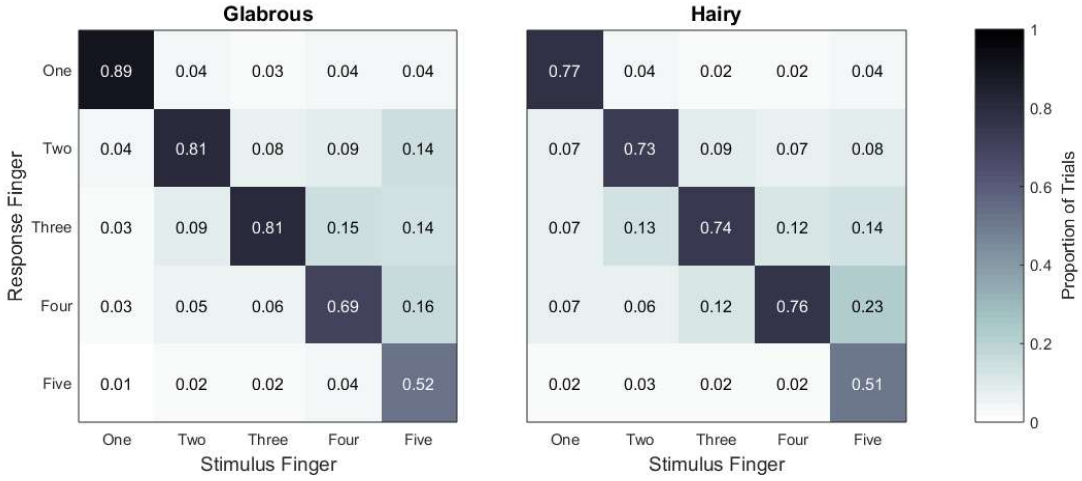

Figure 2.4. Confusion matrices from Experiment 2 showing the proportion of stimuli judged as located on each of the five fingers as a function of which finger was actually stimulated. Fingers were identified by numbers one (the thumb) through five (the little finger). Data from the glabrous skin of the bottom of the fingers is shown in the left panel and data from the hairy skin of the top of the fingers is shown on the right panel. Highly similar patterns of mislocalisations were observed for the two sides of each finger, except for the thumb.

As opposed to the findings on the toes, this directional bias found in the fingers suggests a 'midline' of the hand towards which participants were biased. The equal spatial representation hypothesis proposed by Cicmil and colleagues to explain their results on the toes seems not to explain this bias towards the mid-line of the hand. As the fingers are in reality of roughly equal size, an equal spatial representation hypothesis would not predict any bias in localisation. This is, however, the result we would expect when using suprathreshold tactile stimuli – such as Cicmil and colleagues reported,

localisation of the fingers is extremely accurate when using above-threshold tactile stimuli, which could support an equal spatial representation hypothesis.

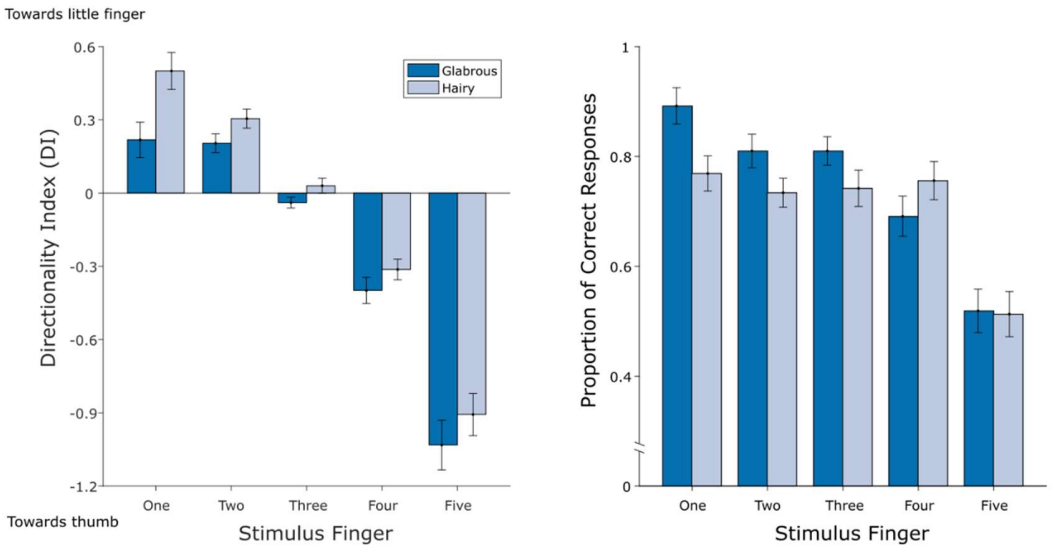

Figure 2.5. Results from Experiment 2. The left panel shows the grand average DI scores for each finger, on the glabrous skin on the bottom of the hand, and hairy skin on the top. The right panel shows the grand average percentage of correct responses made to each finger, on the glabrous skin on the bottom of the hand, and hairy skin on the top. Fingers were identified by numbers one (the thumb) through five (the little finger). Error bars represent the standard error of the mean. Similar patterns of results were found for the two sides of the fingers, for both DI and accuracy.

To further investigate similarities in performance on both skin surfaces, repeated-measures ANOVAs were again performed with two factors: Finger (1 to 5) and Skin Surface (hairy/glabrous). DI and accuracy were tested separately as dependent variables. The first ANOVA indicated that DI was significantly different between the two surfaces of the hand ($F(1,19) = 10.78$, $p < 0.01$, $\eta_p^2 = 0.36$), in contrast to the findings of the correlation. DI was significantly lower for all fingers on the glabrous skin of the hand ($p < 0.05$). However, paired comparisons t-tests between the two skin

surfaces for each finger indicated that the difference between the two skin surfaces was driven by a large effect for the thumb ($t(19) = 3.45$, $p < 0.01$, $d = 0.77$), as other t-tests didn't reach significance when corrected for multiple comparisons ($p > 0.01$). There was again a difference in DI between the five fingers ($F(4,76) = 130.89$, $p < 0.01$, $\eta_p^2 = 0.87$), but no difference in DI depending on which skin surface of each finger was stimulated ($F(4,76) = 1.79$, $p > 0.05$, $\eta_p^2 = 0.09$). As shown in the left panel of Figure 2.5, DI was biased towards the middle finger of the hand, with bias increasing more towards lateral fingers (1 and 5), except for the glabrous surface of the thumb (all $p < 0.05$). A Bayesian repeated-measures ANOVA provided moderate evidence in support of the null hypothesis, that there were no differences in DI for each finger, depending on which skin surface was stimulated ($BF_{01} = 5.97$).

The second ANOVA confirmed overall accuracy again differed depending on which finger was stimulated ($F(4,76) = 30.97$, $p < 0.01$, $\eta_p^2 = 0.62$), but was not different depending on which skin surface was stimulated ($F(1,19) = 3.06$, $p > 0.05$, $\eta_p^2 = 0.14$). A Bayesian repeated-measures ANOVA provided only weak evidence in support of the null hypothesis, that there was no difference in accuracy on the two skin surfaces ($BF_{01} = 1.73$). There was also a significant interaction ($F(4,76) = 3.93$, $p < 0.01$, $\eta_p^2 = 0.17$), indicating that the pattern across fingers differed on the two skin surfaces. Considering the skin surfaces independently, accuracy was not significantly different between the thumb, index and middle finger on the glabrous skin of the hand (all $p > 0.01$), but was between these fingers and the ring and little finger (all $p < 0.01$). In contrast, for the hairy surface of the hand, accuracy was consistent for all fingers from the thumb to the ring finger (all $p > 0.01$), and only different to the little finger (all

$p < 0.01$). Paired samples t-tests, however, confirmed that differences in accuracy were only significant between the hairy and glabrous skin of the thumb ($t(19) = 3.72$, $p < 0.01$, $d = 0.83$).

These results suggest that, as for the toes, tactile localisation of the fingers is biased as a result of inaccuracies in high-order body representation used during tactile-spatial remapping, as shown by consistent biases towards the middle finger of the hand. The results of this study are also consistent with previous studies investigating tactile acuity across the fingers, which showed that sensitivity decreases from the thumb to the little finger (Duncan & Boynton, 2007; Sathian & Zangaladze, 1996; Vega-Bermudez & Johnson, 2001). This occurred as a result of decreasing cortical magnification (the proportion of cortical area given the skin area on the body) across representations in S1 from the thumb to the little finger, similar to macaques (Duncan & Boynton, 2007; Sutherling, Levesque, & Baumgartner, 1992). However, our results indicate that this pattern is only consistent across the two skin surfaces of the four fingers, not including the thumb. There were less localisation errors on the glabrous skin than on the hairy skin of the thumb, which reduced the strength of bias (as it is the outermost finger) and increased accuracy (as is shown in our results).

Shared individual differences across the two sides of the fingers

The results above show that there are similar patterns of mislocalisations on the two surfaces of the fingers at the level of grand averages, as well as the toes. We also investigated whether idiosyncratic differences across participants are also common to the two sides of the fingers, using the same method described in Experiment 1.

On average, classification accuracy was 74.61%, significantly higher than chance performance, $t(19) = 4.63$, $p < 0.001$, $d = 1.04$. Across participants, classification accuracy ranged from 13.16% to 100%, but exceeded 50% in 19 of 20 participants. This provides strong evidence for shared individual differences in mislocalisation patterns on the two surfaces of the fingers, as well as the toes. Although the pattern of mislocalisations appears to be consistent on the fingers (if not the thumb), there are again individual differences in mislocalisations that are consistent across the two skin surfaces for each participant. This supports our novel finding that participants show consistent patterns in mislocalisation across the two skin surfaces at the group level also.

Effect of previously stimulated finger on current finger identification

We again investigated the effect of identity of the previously stimulated digit on directionality index scores for fingers 2, 3 and 4. Finger 1 and 5 were again used as "previously stimulated fingers" to remain consistent across our analyses, despite accuracy for finger 5 being poorer than the other fingers (0.52 and 0.51 respectively). Response data for the two surfaces of the hand was grouped according to which finger has been stimulated on the immediately preceding trial, and DI and accuracy were calculated.

On both skin surfaces, when the immediately preceding touch was on finger 1, mean DI values for finger 2 were close to zero (hairy: 0.04, glabrous: 0.08), there was little bias in participant's responses. DI scores for fingers 3 (hairy: -0.15, glabrous: -0.15) and 4 (hairy: -0.45, glabrous: -0.76) when preceded by finger 1 were greater than in our original analysis, indicating a stronger bias in responding towards finger 1. When

the immediately preceding touch was on finger 5, mean DI scores for fingers 2 (hairy: 0.44, glabrous: 0.29) and 3 (hairy: 0.1, glabrous: 0.01) were marginally greater than in our original analyses, indicating a bias in responding towards finger 5. Mean DI scores for finger 4 when immediately preceded by finger 5 were only marginally weaker than in our original analysis (hairy: -0.29, glabrous: -0.4), showing a slight bias in responding towards finger 5. DI was significantly different depending on whether finger 1 or 5 was previously stimulated on the hairy skin of fingers 2 (paired t-test, $t(19) = -3.46$, $p < .01$, $d = 0.85$) and 3 (paired t-test, $t(19) = -4.86$, $p < .01$, $d = 0.39$). Compared to finger 1, finger 5 may have had a weaker biasing effect when it was the previously stimulated finger as accuracy in localising this finger was poor – if participants did not correctly localise finger 5, it would not bias responses on the next trial.

Error rates again differed depending on which finger was stimulated on the immediately preceding trial. On both skin surfaces error rates were greatest for finger 2 following stimulation of finger 5, for finger 3 following finger 1 or 5, and for finger 4 following finger 1. Number of errors was not significantly different depending on whether finger 1 or 5 was previously stimulated for any fingers (paired t-tests: $p > .01$ in all cases). As for the toes, this pattern of results indicates that touches farther from the preceding digit result in a greater number of erroneous responses. This finding also corroborates our earlier assertion that participants' responses are biased towards the midline of the hand, as identification of finger 3 was equally disrupted by touches to either finger 1 or 5.

We again investigated whether DI was significantly different on the two skin surfaces of the fingers depending on the previously stimulated fingers. Repeated-

measures ANOVAs were performed with two factors: Previously Stimulated Finger (1 to 5) and Skin Surface (hairy/glabrous). Each of the currently stimulated fingers (2, 3 and 4) were tested separately as dependent variables. Each finger showed a significant effect of Previously Stimulated Finger, (finger 2: $F(4, 76) = 8.94$, $p = 0.001$, $\eta_p^2 = 0.69$, finger 3: $F(4, 76) = 4.20$, $p = 0.02$, $\eta_p^2 = 0.51$, finger 4: $F(4, 76) = 3.59$ $p = 0.03$, $\eta_p^2 = 0.47$), in line with our previous results. None of the fingers were significantly different depending on which skin surface was stimulated (finger 2: $F(1, 19) = 3.82$, $p = 0.07$, $\eta_p^2 = 0.17$, finger 3: $F(1, 19) = 2.10$, $p = 0.16$, $\eta_p^2 = 0.10$, finger 4: $F(1, 19) = 3.16$, $p = 0.09$, $\eta_p^2 = 0.14$), and none of the interactions were significant (finger 2: $F(4, 76) = 9.32$, $p = 0.45$, $\eta_p^2 = 0.05$, finger 3: $F(4, 76) = 0.87$, $p = 0.48$, $\eta_p^2 = 0.04$, finger 4: $F(4, 76) = 2.41$, $p = 0.06$, $\eta_p^2 = 0.11$). This provides further evidence that characteristic patterns of mislocalisation are highly consistent across the hairy and glabrous skin surfaces of the fingers.

2.4. General Discussion

We investigated patterns of confusion for localisation of tactile stimuli on glabrous and hairy skin surfaces of the toes (Experiment 1) and fingers (Experiment 2). This study yielded three main findings: (1) We replicated the distinct patterns of mislocalisations on the glabrous skin of the fingers and toes; (2) We found that the respective patterns are consistent on the hairy skin of the fingers and toes; and (3) We showed that despite these patterns being very consistent across participants, there are idiosyncratic differences in participant's performance that can predict performance across the two skin surfaces. In addition, we replicated the finding that localisation is

biased towards the previously stimulated toe (Cicmil et al., 2016). We showed that this bias is consistent over the glabrous and hairy skin of both the fingers and toes. To our knowledge, this is the first quantitative comparison of tactile mislocalisation over the two skin surfaces of the fingers or toes. The similar patterns on each surface of the digits indicate that biases in tactile mislocalisation occur at the level of complete digits, as opposed to individual skin surfaces. As such, they likely arise in higher-order representations of the body, where the body is represented as a fully-3D, volumetric object (Longo, 2014). This supports conclusions from previous studies, that disturbances in tactile localisation arises from distortions of high-level representations of the body structure (Anema et al., 2008; Cicmil et al., 2016).

Cicmil et al. (2016) describe the directional distortions when localising the toes as arising from inaccuracies in the underlying body image. They suggest that the toes are represented as being of equal sizes, although in reality the big toe is much larger than the remaining toes in order to support bipedal walking (Napier, 1967). From this hypothesis we would predict a high number of mislocalisations, and directional bias of these mislocalisations, exactly as found in this study: the second and third toes are biased towards the little toe, and the fourth towards the big toe. In support of this account, macaques have roughly equal spacing of the toes and show directional mislocalisation of touch similar to the human hands, i.e. towards the middle digit (Vierck, Favorov, & Whitsel, 1988). This perhaps reflects that primates use their feet both for locomotion, as in humans, and for grasping, as the human hand is used (Holowka, O'Neill, Thompson, & Demes, 2017b).

When using a near-threshold stimulus, the stereotypical pattern of mislocalisations found over the fingers still differs from that on the toes: mislocalisation of the fingers is always biased towards the middle finger. This bias is even evident when the additional bias towards the previously stimulated finger is considered. As the distribution of digit size across the hand is more symmetrical than the foot, this pattern of results may be expected if hand representation was distorted to give equal size weighting to each finger. Interestingly, our results indicate that the thumb is included in the hand schema, as it is biased towards the middle finger in the same way as the other fingers. Previous research has indicated that the index finger, rather than the thumb, is perceived as analogous to the big toe (Singh, 1990), indicating that the thumb is perceived differently, in some way, to the rest of the fingers. In the present study, the hairy skin of the thumb showed significantly weaker biases towards the midline of the hand, perhaps indicating a less robust representation of the thumb in relation to the other fingers. This pattern of results may also reflect a bias in selecting points towards the midline of the hand, like the bias in selecting points towards the midline of the torso (Ho & Spence, 2007). As for the fingers, bias towards the midline of the body increases the farther from the midline the tactile stimulus is applied. This effect persists even when the bias towards the previously stimulated finger is accounted for: our results show that even if the previously stimulated finger is away from the midline of the hand, biases continue to be in the direction of the midline (although the strength of bias is attenuated by the immediately preceding touch). Yet it cannot be determined from these results whether the bias towards the hand or body midline is a product of distortions of the underlying body image, or a bias in decision-making for uncertain cases.

Critically, our findings do not reflect the pattern of results that may arise if performance was based solely on differences in tactile acuity across the fingers. A number of studies have shown that tactile acuity of the glabrous skin of the fingers decreases from the thumb to the little finger, as a result of decreasing cortical magnification across representations in S1 from the thumb to the little finger (Duncan & Boynton, 2007; Sathian & Zangaladze, 1996; Sutherling et al., 1992; Vega-Bermudez & Johnson, 2001). While we do not measure tactile acuity directly, we do have a measure of localisation accuracy. Our second experiment extends previous results, showing a similar pattern on localisation accuracy as spatial acuity across the fingers, and moreover confirming that this pattern is the same over the hairy skin and glabrous skin, apart from on the thumb. Sensitivity of the toes is different: localisation accuracy is high for the big and little toes, but consistently low on the glabrous skin of the middle three toes (Cicmil et al., 2016). Our own accuracy results corroborate these findings on the toes, and suggest that accuracy is similar across the glabrous and hairy surfaces. Importantly, these results differ from the patterns of bias found on the fingers and toes, confirming that the bias found relates to distortions in higher-order representations of the body, not low-level sensory processing.

Previous studies, however, have shown different patterns of mislocalisation bias on the two skin surfaces of the hand. Mancini et al. (2011) found consistent distal and radial biases in localisation (towards the knuckles and the thumb). Weaker proximal biases (towards the central point of the palm) are found on the palm of the hand. Mancini and colleagues suggest that both high- and low-level processes are involved – the greater magnitude of distortions on the dorsum is attributable simply to lower spatial

resolution of the receptive fields, comparable to the palm (Ackerley et al., 2014; Johansson & Vallbo, 1979; Mancini et al., 2011), whereas the differences in direction of the bias is attributed to differences in the underlying 2-D representations of the individual skin surfaces (Longo, Mancini, & Haggard, 2015; Mancini et al., 2011). However, these findings do not necessarily conflict with our results. While localisation on the palm and dorsum of the hand relies solely on the fragmented implicit representation of the hand, finger localisation also relies on proprioceptive information about the variable position of the fingers. For example, recent research has shown that finger posture alters our structural body representation to account for changing position (Tamè, Dransfield, et al., 2017). Moreover, localising touch in external space uses a distorted body representation common to the underlying position sense, as opposed to tactile localisation (Longo, Mancini, et al., 2015). This body representation underlying position sense and tactile spatial remapping necessarily is a fully 3-D representation of the body as it appears in external space (Longo & Haggard, 2012). As such, the fingers may be represented as fully 3-D objects when localising tactile stimuli as we also need to account for their position when localising touch.

This reliance on position sense when localising touch may also account for the subtle differences found across the hairy and glabrous skin of the fingers, as posture was altered when testing the two skin surfaces. We found that DI was marginally lower on the glabrous skin than the hairy skin of all the fingers, indicating biases towards the thumb on the glabrous skin, and towards the little finger on the hairy skin. We also found this slight difference in direction bias on the two skin surfaces while evaluating the effect of previously stimulated finger on current finger identification. When the

middle finger was stimulated twice in a row, identification of the finger was biased in opposite directions for the two skin surfaces – towards the thumb on the glabrous skin, and the little finger on the hairy skin. Although this difference was not significant, it shows a trend in the same direction as our original analysis. Despite these slight differences, we show that the pattern of biases across the fingers is highly consistent on the two skin surfaces. Moreover, due to the changing position of the hand, the differences in DI on the two skin surfaces described above result in biases in the same direction in external space – directed away from the body midline on both the hairy and glabrous skin. This provides further support to our conclusion that we rely on a 3-D representation of the body positioned in external space when localizing touch on the fingers specifically, as we find biases of the same direction in external space, as well as of the same pattern of the two skin surfaces, regardless of hand posture.

We obtained confusion matrices showing the pattern of mislocalisation between toes and fingers on both the glabrous and hairy surface of the foot and hand. This showed that the distinct patterns of mislocalisation biases are highly consistent over the hairy and glabrous skin of the fingers and toes. Although this pattern was highly stereotyped, we found individual differences in each participants' performance, which supports a 3D representation of the individual fingers and that these distortions arise in high-level body representation, rather than low-level somatosensory processing.

Chapter 3: A common representation of fingers and toes

3.1. Introduction

The human hands and feet are serially homologous structures that have co-evolved (Rolian et al., 2010), resulting in numerous similarities between the two body parts. They have an identical number of homologous digits (Lewis, 1989), a common overall bone structure (Owen, 1849/2008), and distinct hairy and glabrous skin surfaces on their alternate sides (Lewis, 1989; Mountcastle, 2005). However, there are also obvious and profound differences between the hands and feet in humans. Both body parts have become highly specialised by evolution for distinct functions (McNutt, Zipfel, & DeSilva, 2018; Tocheri, Orr, Jacofsky, & Marzke, 2008), and have gross differences in shape, and distinct representations in the somatosensory cortex in both monkeys (Hashimoto et al., 2013; Merzenich et al., 1978; Nelson et al., 1980) and humans (Akselrod et al., 2017; Disbrow, Roberts, & Krubitzer, 2000; Fox et al., 1987; Hashimoto et al., 2013). Not only are representations of the hands and feet distinct in S1, they vary in their somatotopic organisation – a number of studies have shown that the fingers are ordered along the medio-lateral axis of the postcentral gyrus (Kolasinski et al., 2016; Martuzzi et al., 2014; Schweizer et al., 2008), no somatotopy was found for the toes, as well as lower selectivity in responding to each individual toe compared to the individual fingers (Akselrod et al., 2017).

Beyond comparisons of the physical and functional properties of the hands and feet, it is unclear how high-level mental representations of these two body parts are related, although there are hints in the literature towards there being deep functional

connections. One line of evidence for this comes from Gerstmann syndrome (Gerstmann, 1939), in which some patients show specific deficits in identifying digits, whether fingers or toes (Mayer et al., 1999; Tucha et al., 1997). Another line of evidence comes from recent studies of tactile localisation in healthy adults, which have identified distinct patterns of confusions between the fingers and toes, but with some similarities in mislocalisations (Cicmil et al., 2016; Manser-Smith, Tamè, & Longo, 2018; Schweizer et al., 2001; Tamè, Wühle, et al., 2017). For example, digits of both the hands and feet are more frequently mislocalised to neighbouring than distant digits, however not equally to each neighbouring digit, but more often in the direction of the central digits of the hand or foot (Cicmil et al., 2016; Manser-Smith et al., 2018). These similarities in tactile mislocalisation of the digits indicate that there may be commonalities in mental representations of the hands and feet, despite their divergent physical and functional properties. However, this has not been supported by a direct comparison of the representations of fingers and the toes in the same individuals.

In a recent study (Manser-Smith et al., 2018), we investigated whether the patterns of confusion between digits arise from relatively low-level representations, such as somatotopic maps in primary somatosensory cortex (SI), or from higher-level representations of the body. Given that somatotopic maps have distinct representations of the glabrous and hairy skin surfaces of the hands and feet (Merzenich et al., 1978; Nelson et al., 1980), mislocalisations between digits arising from SI may show different patterns on each skin surface, resulting from idiosyncrasies in somatotopy of S1. In contrast, if digit confusions arise from higher-level representations of the body as a coherent, volumetric whole (wherein each digit is a single unit that happens to contain

the two skin surfaces), then similar patterns of mislocalisation should be found on each skin surface. We found that confusion matrices were highly similar on the glabrous and hairy surfaces of both the toes (Experiment 1) and fingers (Experiment 2). Moreover, we used a form a representational similarity analysis (RSA; Kriegeskorte, Mur, & Bandettini, 2008) to investigate whether individual differences between participants are shared across the glabrous and hairy skin surfaces of each limb. We showed that idiosyncratic differences in the pattern of mislocalisation on one skin surface predicted such patterns on the other skin surface, for both the fingers and toes. Together these results suggest that mislocalisations arise at the level of complete digits, not of individual skin surfaces, consistent with their arising from higher-level body representations.

In this study we investigated whether there are individual differences in patterns of tactile localisation that are shared between the fingers and toes, applying the logic of our previous study. That is, we used RSA to determine whether idiosyncratic person-to-person differences in the pattern of confusions between fingers predict such differences in the confusions between toes, and vice versa. As the identification of shared individual differences between the two skin surfaces of the fingers and toes suggested that mislocalisations arise from a high-level representation of the digits as single units (incorporating both skin surfaces), individual differences shared between the fingers and toes would suggest that there are shared high-level representations of the hands and feet. All procedures, including sample size, exclusion criteria, and analysis plans were pre-registered on the Open Science Framework (OSF; osf.io/4kdte).

3.2. Methods

Participants

In our previous study (Manser-Smith et al., 2018), the individual differences found between the two surfaces of the fingers and toes using our decoding approach showed Cohen's *d*'s of 1.76 and 1.04, respectively. As we reduced the number of trials completed by each participant in the present experiment (due to time constraints during testing), and we expected a weaker effect than in our previous study because we were comparing two different body parts, we conducted a power analysis using an effect size of half the smaller value found in our previous study. We based our calculations on a one-tailed t-test, as we have a clear directional prediction that classification accuracy should be greater than chance levels, rather than lower than chance. As such, we conducted a power analysis using G*Power 3.1 (Faul et al., 2007), a Cohen's *d* of 0.52, an alpha value of 0.05, and power of 0.90, which indicated that 34 participants were required.

To use a round number, we recruited 40 participants (22 female; mean age = 27.2 years; SD = 8.27). Thirty-nine participants were right-handed, and one left-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971); mean = 60.8, range = -13 – 100). Of the 39 right-handed participants, 38 were right-foot dominant and one participant was not dominant for either foot. The one left-handed participant was also left-foot dominant, as assessed by the Waterloo Footedness Questionnaire (Elias et al., 1998); mean = 38.0, range = -75 – 100). EHI and WFQ scores were strongly correlated across participants, $r = 0.66$, $p < 0.001$. All participants gave written

informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

Stimuli

In our previous study, two different types of tactile stimuli were used to stimulate the fingers and toes. The tip of the experimenter's finger was used for the toes, and a von Frey hair for the fingers. As the fingers have low pressure sensitivity thresholds in comparison to the toes, a near-threshold stimulus is needed to give a clear pattern of mislocalisations (Schweizer et al., 2000) and avoid ceiling effects such as encountered by Cicmil et al. (2016). However, given the aims of the present study, it was critical to use a consistent type of tactile stimulation across the fingers and toes. As such, tactile stimuli were delivered to both the fingers and toes using von Frey hairs. The strength of von Frey hairs to be used was determined at the beginning of the experiment using the same procedure as in Experiment 2 of our previous study (Manser-Smith et al., 2018). Five strengths of von Frey hair were tested, from 0.008g to 0.16g for the hand. For the foot, five strengths of von Frey hair from 0.04g to 0.6g were used, as during pilot testing most participants could not localise above chance (i.e., 50%) of touches using the same stimuli that were used on the fingers. We stated in our pre-registered plan that if the participant was not performing well enough using the five von Frey hairs stipulated previously, progressively stronger von Frey hairs were tested until they were performing at the required level (70% correct responses). However, this issue did not arise with any participants. The mean strength von Frey hair used on the hands was 0.018g, (range = 0.008g – 0.04g), and on the feet was 0.19g (range = 0.04g – 0.6g).

During the stimulus identification procedure, participants received tactile stimulation on the top of every digit of the left hand or foot in a random order, by each von Frey hair, starting from the weakest strength. Once the digits had been tested with the strongest von Frey hair the procedure was reversed, reducing the strength of the von Frey hair to the weakest again. This staircase was carried out twice, and the percentage of correct responses was calculated for each strength of von Frey hair across all digits. The weakest strength von Frey hairs that participants could correctly localise above 70% of touches were used in the experiment. This threshold was chosen as it was greater than chance performance, but still provides a sufficient number of mislocalisations for us to measure. As the fingers and toes have quite different sensitivity thresholds (Mancini et al., 2014; Weinstein, 1968), the strength of von Frey hair used was determined separately for the fingers and toes. Moreover, although tactile acuity differs significantly across the fingers (Duncan & Boynton, 2007; Sathian & Zangaladze, 1996) and toes (Manser-Smith et al., 2018), for ease of testing and consistency with our previous study, one strength of von Frey hair was used across all five fingers/toes.

Task

The testing procedure closely resembled that used in our previous study (Manser-Smith et al., 2018). All participants were tested on their left hand and foot, regardless of assessed hand and foot dominance. Figure 3.1 shows participant's posture during testing: they were seated in a comfortable position with their left foot resting on a stool, and their left hand resting palm-down on a table. This posture was kept consistent regardless of whether the hand or foot was being tested, and they were instructed to

remain as still as possible throughout each experimental block. The experimenter used a von Frey hair to apply tactile stimulation to the dorsal surface of the participant's toe, between the metatarsophalangeal joint (at the base of the toe) and the interphalangeal joint (in the middle of the toe), or the medial phalanx of the finger or proximal phalanx of the thumb, for about 500ms. One finger or toe was stimulated per trial. Participants responded by verbally identifying which digit they felt had been touched. Digits were identified by numbers 1 to 5: the big toe or thumb corresponding to number 1, to the little toe or finger corresponding to number 5. Touch was only applied to the hairy skin, and not the glabrous skin. The hairy skin was chosen because we found in our previous study that participants find it to be more comfortable to sit in the position where the hairy skin can be tested. Vision was prevented throughout the experiment using a blindfold.

The experiment consisted of four blocks, two in which the fingers were stimulated and two in which the toes were stimulated. ABBA counterbalancing was used to vary order of presentation, with the first condition counterbalanced across participants. Each block contained 100 trials, 20 for each of the 5 digits, resulting in 400 total trials completed by the participant. The order of digit stimulation was pseudo-randomised within each block of trials, so that there was an approximately equal number of each type of preceding trial.

Figure 3.1. Experimental set-up. Participants sat in a chair with their left foot resting on a foot rest, and their left hand resting on a table. This posture gave the experimenter easy access to both the fingers and toes. Vision was prevented using a blindfold.

Analysis

The analyses carried out closely resembled those of our previous study, and were exactly as described in the pre-registration document. Two confusion matrices were obtained per participant, one showing the pattern of mislocalisations on the hairy skin of the fingers, and the other showing the pattern of mislocalisations on the hairy skin of the toes. Each confusion matrix is a 5x5 grid where each column represents stimuli applied to one digit, and each row represents the proportion of trials on which the participant judged that one digit was touched. As such, the confusion matrix nicely shows the proportion of correct localisations, as well as the pattern of mislocalisations between digits.

In order to obtain a single value which indicates both direction and magnitude of bias in toe selection we used the directionality index (DI) developed by Cicmil and colleagues (2016), as in our previous study. For each digit the mean of the responses given to identify which digit was stimulated was calculated, minus the actual digit number of the stimulated toe, as shown in Equation 1:

Equation 1. DI = (mean of response digit numbers - stimulated digit number).

One-sample t-tests were carried out to assess whether DI scores of the central three digits of the hand and foot were significantly different from zero. Response accuracy was also analysed as DI scores of zero (no bias in responding) may occur in two different scenarios. Firstly, if responses to stimulation of a toe were entirely accurate. Secondly, if participants had responded equally to neighbouring toes, for example toes 2 and 4 when toe 3 was stimulated. As such accuracy was also used as a measure of performance on the task. The analysis of response accuracy can be found in Supplementary Material.

The key novel question of this study was whether idiosyncratic person-to-person differences in the pattern of confusions between digits are shared between the fingers and toes. To isolate individual differences in each participant we used a leave-one-participant-out procedure, identical to that was used previously to show that confusions arise from a common representation of the two sides of the hand/foot (Manser-Smith et al., 2018). We regressed the 20 off-diagonal cells (i.e., the localisation errors) of each

participant's confusion matrix (C_i) on the grand average confusion matrix for the other 39 participants (C_{GA}), as in Equation 2.

Equation 2: $$\widehat{C}_i = \beta_1 C_{GA} + \beta_0$$

The regression parameters ($ß_1$ and $ß_0$) were calculated using standard least-squares methods as the values that minimised the sum of squares of the residual values that is the difference between the fitted values and the actual values, as in Equation 3.

Equation 3: $$residuals_i = \widehat{C}_i - C_i$$

These residuals quantify the way in which a given participant's confusion matrix differs idiosyncratically from the pattern shown by the other participants. Critically, this procedure eliminates differences between participants in overall levels of accuracy, isolating the *pattern* of confusions between fingers and toes, rather than overall performance. These residuals were calculated separately for the confusion matrices on the fingers and the toes, resulting in two sets of residuals per participant.

If there are shared individual differences between the fingers and the toes, the two sets of residuals for a given participant should be similar. That is, a participant who differs idiosyncratically from other people on the fingers should also differ in the same way on the toes. To assess this, we used a cross-correlation classification procedure. For each participant, we calculated the correlation between the two patterns of residuals, the within-participant cross-correlation. Then we calculated the 78 cross-correlations

comparing each of that participant's two patterns to the opposite pattern of each of the other 39 participants. Classification accuracy was calculated for each participant as the percentage of those 78 between-participant correlations which were smaller than the within-participant cross-correlation. High classification accuracy indicated that there were fewer incidences when participants were more like others' scores than their own scores, and low classification accuracy indicated that there were more incidences when participants were more like others' scores than their own scores. Our preregistered analysis plan specified a one-sample t-test to assess whether classification accuracy was significantly greater than chance (i.e. 50%). We used a one-tailed test given that we had a clear directional prediction for greater than chance classification (indicating individual differences were stronger within- than between-participants). We also carried out a Bayesian one-sample t-test to assess whether the null hypothesis (H_0) should be accepted over the alternative hypothesis (H_1). This was done using the default parameters in JASP 0.8.2.0 (Wagenmakers et al., 2018).

The data associated with this research are available through the OSF (osf.io/mh9xs).

3.3. Results and discussion

Directional bias for localisation of the toes

Figure 3.2 (left panel) shows the confusion matrix for tactile toe localisation on the hairy skin of the toes. As in our previous study, the majority of mislocalisations were made onto neighbouring toes. Toe identification errors were not randomly distributed across toes but biased towards the lateral side of the foot for toe 2 (*M:* 0.37, SD: 0.21),

$t(39) = 11.00$, $p < 0.0001$, $d = 1.76$, and toe 3 (*M:* 0.20, SD: 0.20), $t(39) = 6.35$, $p < 0.0001$, $d = 1.00$. For toe 4, there was a significant medial bias (*M:* -0.16, SD: 0.14), $t(39) = -7.45$, $p < 0.0001$, $d = -1.14$. These results provide a direct replication of the results of our previous study and of Cicmil et al. (2016), corroborating the presence of directional biases for tactile toe localisation in response to stimulation of the hairy skin of the toes.

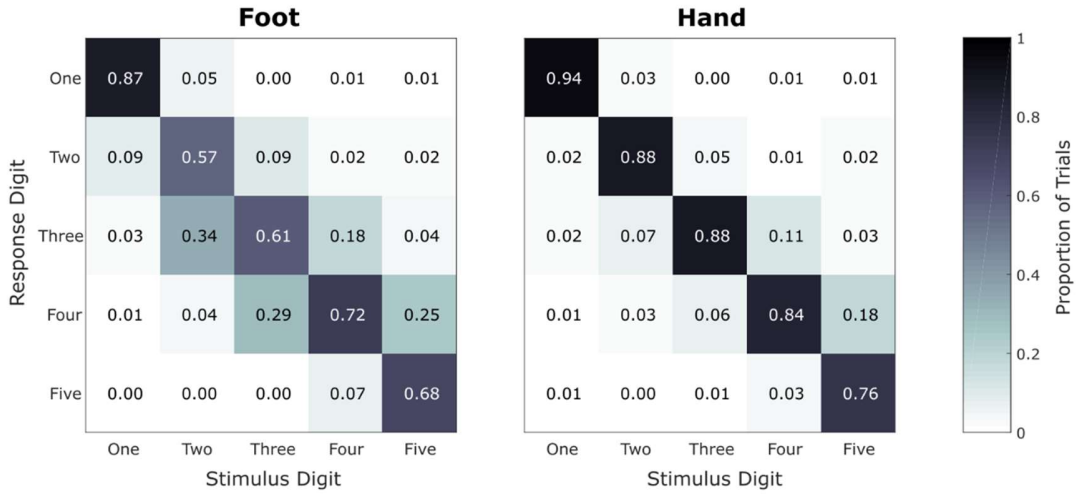

Figure 3.2. Confusion matrices showing the proportion of stimuli judged as located on each of the five digits as a function of which digit was actually stimulated. Digits were identified by numbers one (the big toe/thumb) through five (the little toe/finger). Data from the foot is shown on the left panel, and data from the hand is shown in the right panel. The proportion of correct responses for each digit is shown along the diagonal from the top-left to the bottom-right. The off-diagonal cells represent mislocalisations between digits.

Directional bias for localisation of the fingers

Figure 3.2 (right panel) shows the confusion matrix for tactile finger localisation on the hairy skin of the fingers. Finger identification errors were not randomly distributed, but biased towards the little finger for the index finger (*M:* 0.11, SD: 0.17), $t(39) = 3.92$, $p < 0.0001$, $d = 0.65$, and towards the thumb for the ring finger (*M:* 0.03,

SD: 0.10), $t(39) = -7.56$, $p < 0.0001$, $d = 0.30$. There was no selection bias for the middle finger (*M:* -0.13, SD: 0.11), $t(39) = 1.94$, $p = 0.06$, $d = -1.18$, suggesting that lateral or medial fingers were chosen interchangeably. Once again, these results provide a direct replication of the results of our previous study, that there are consistent directional biases for tactile finger localisation in response to stimulation of the hairy skin of the fingers.

Shared individual differences between the fingers and the toes

The key question was whether person-to-person differences in the pattern of mislocalisations is shared between the fingers and toes. On average, classification accuracy was 59.25%, which was significantly above chance (i.e., 50%), $t(39) = 2.29$, $p = 0.01$, $d = 0.36$. A Bayesian one-sample t-test provided moderate evidence in support of the alternative hypothesis against the null hypothesis, $BF_{10} = 3.56$. Across participants, classification accuracy ranged from 0% to 95%, but exceeded 50% in 26 out of 40 participants. As classification accuracy was only marginally above chance on average, and was not above chance in 14 of 40 participants, we performed an additional analysis to those described in the preregistration of this study. We calculated the bootstrapped 95% confidence intervals (CIs), resampling 10000 times with replacement, to estimate the likelihood of replicating our present results of above chance classification accuracy. The lower and upper bounds of the bootstrapped CIs were 51.38% and 67.00%, respectively. This result provides evidence for shared individual differences between the fingers and toes in how people mislocalise touch on the digits.

These idiosyncratic differences between people are apparent despite there being distinct patterns of mislocalisation bias found on the fingers and toes.

3.4. Discussion

These results provide evidence for a common representation of fingers and toes. We investigated whether there are shared individual differences in patterns of confusion for localisation of tactile stimuli on the fingers and the toes. We found that idiosyncratic differences in participants' performance were shared between the fingers and toes, despite the overall different patterns of localisation bias found on these two body parts, suggesting that idiosyncratic differences arise from a single representation of the digits, as opposed to separate representations. As such, this result suggests that there is a shared representation of the fingers and toes, despite their differences in form (i.e., morphological structure) and use (i.e., motor function). Moreover, we replicated the distinct patterns of tactile confusion found on the digits of the hand and the foot found in previous studies (Cicmil et al., 2016; Manser-Smith et al., 2018; Schweizer et al., 2001).

In a recent study (Manser-Smith et al., 2018) we found that there are idiosyncratic differences in patterns of tactile confusions that are shared between the two skin surfaces of the fingers and toes. From this finding we concluded that individual differences in mislocalisations may arise from higher-level representations of the body as a single, volumetric whole, as opposed to arising from distinct somatotopic maps of the two skin surfaces. In the present study we also identified individual differences in performance that are shared between the fingers and toes. Following the logic of our previous study, we suggest that there is a single high-level representation of the fingers

and toes from which mislocalisations arise. Such a shared representation indicates that deep functional connections between the hands and feet are preserved from their co-development in humans (Rolian et al., 2010), despite their present differences in shape and use, as evidenced by clinical cases such as both finger and toe agnosia occurring in Gerstmann syndrome (Mayer et al., 1999; Tucha et al., 1997).

A shared high-level mental representation of the hands and feet may have developed to be beneficial to our primate ancestors, and would still beneficial to primates that retain similar structure and functional use of the hands and feet, to facilitate co-ordinated use. For example, chimpanzees (our closest primate relatives) retain relatively mobile ankle joints compared to humans, and fully abducted hallux (the big toe) similar to the thumb (McNutt et al., 2018). For arboreal and terrestrial quadrupedal monkeys such as chimpanzees, the hands and feet share many functions such as grasping and propulsion during locomotion (Rolian, 2009; Schmitt et al., 2016; Szalay & Dagosto, 1988), although there is evidence for divergent use occurring during reaching tasks (Hunt, 1994). In contrast, although humans may co-ordinate use both the hands and feet to perform an action (Dietz, 2002), they do not share the same functional role in reaching the desired outcome. As such, although a shared mental representation of the hands and feet would have been evolutionarily beneficial to non-human primates to facilitate co-ordinated actions it may not be as advantageous to modern humans.

This may be reflected in the relatively weaker classification performance in the present study comparing fingers and toes (59.3%) than that found in our previous study (Manser-Smith et al., 2018) comparing the hairy and glabrous surfaces of the toes (82.4%) and fingers (74.6%). In our previous study we found strong idiosyncratic

differences in the tactile localisation task comparing performance on the two skin surfaces of the hand or foot, providing strong evidence that there is a shared mental representation of the two skin surfaces of the hands and feet (such as a volumetric 3-D model of the body part). The individual differences found in the present study are significant but relatively weaker than in our previous study, perhaps indicating the diminished benefit of having a shared representation of the hand and the foot when form and use are as different as they are in humans. This suggests that, despite overlap, the representations of the fingers and toes are at least partly distinct, reflecting the divergent structure and function of the hands and feet in modern-day humans.

One important point to note is that the common representation of the hands and feet is not necessarily a common representation of both body sides. In the present study only the left hand and foot was tested, therefore we can only suggest that there is a common representation for the single body side. However, it is possible that a shared representation of the hands and feet may also be shared across both sides of the body. A number of studies have shown that tactile stimuli applied to one hand can interfere with touch localisation on the other hand (Braun, Hess, Burkhardt, Wühle, & Preissl, 2005; Tamè, Braun, Holmes, Farnè, & Pavani, 2016; Tamè et al., 2011), possibly resulting from bilateral hand representation in postcentral somatosensory cortex (Iwamura, 2000; Iwamura et al., 1994), or another representational stage at which the differentiation between the two hands is less clearly defined (Tamè et al., 2011). While we are not aware of any studies that show either that there is bilateral foot representation, or interference in tactile localisation between the two feet, these findings for the hands

suggest that there could be a common representation of the hands and feet that also does not distinguish between body side.

One possible explanation of our results is that shared idiosyncratic differences in localisation are a result of systematic biases for the perception of space in general, instead of for specific body parts. There are numerous studies that show how the body's position in external space can influence ability to perceive tactile stimuli on the body, for example crossing the hands (Yamamoto & Kitazawa, 2001), feet (Schicke & Röder, 2006), and fingers (de Haan et al., 2012) reduces our efficiency in localising touch on these body parts. These findings demonstrate how the representation of the body as a 3-dimensional object is intrinsically linked to our perception of it in relation to the external space that it inhabits. In the present experiment, we suggest that idiosyncratic biases in localisation may arise from higher-level representations of the limbs as 3-D objects such as this. To attempt to disentangle how the body representation itself and the body's position in external space contribute to localisation biases, future experiments may focus on manipulating posture of the fingers and toes relative to one another, or relative to the gaze-direction, for example. However, it seems unlikely that biases in the perception of space in general would produce such specific patterns of confusions between the fingers and toes as we have found in this and previous studies.

It is also possible that the biases we describe may arise from post-perceptual decision-making processes, as opposed to tactile perception per se. From the results of this experiment and others we have suggested that patterns of tactile confusions may arise from high-level body representations, which likely originate in the posterior parietal cortex. Studies of perceptual decision-making in the somatosensory system have

found that at successive processing stages from SI, to SII, to the posterior parietal cortex, that neuronal activity correlates progressively less with processing of the tactile stimulus itself and more with the animal's behavioural decision (e.g., de Lafuente & Romo, 2006; Romo, Lemus, & de Lafuente, 2012). As such, the findings of our experiment may reflect the organisation of a mental representation of the limbs which is used by participants to transform the raw sensory information they receive into a perceptual decision about which digit was stimulated. Overall, the distinction between perceptual and decision-making processes is not a clear one, in relation to localising tactile stimuli on the body.

Overall, in this study we showed that idiosyncratic differences in performance on a tactile localisation task can be identified between the fingers and the toes, despite their divergent form and use. This provides the first evidence that there is a shared high-level mental representation of the fingers and toes. Such shared structure may relate to the ability for compensatory use of the feet for skilled behaviours in one-handed individuals (Hahamy et al., 2017).

Chapter 4: A common representation of the left and right fingers

4.1. Introduction

Localising tactile stimuli on the body is a fundamental function of the somatosensory system. However, there is a large body of evidence that suggests this function is systematically biased on a number of different body parts, including the toes (Cicmil et al., 2016; Manser-Smith et al., 2018; Manser-Smith, Tamè, & Longo, 2019), the dorsum of the hand (Culver, 1970; Mancini et al., 2011; Margolis & Longo, 2014; Nathan & Rice, 1966), and the forearm (Parrish, 1897; Sadibolova, Tamè, & Longo, 2018; Steenbergen, Buitenweg, Trojan, Klaassen, & Veltink, 2012; Steenbergen, Buitenweg, Trojan, & Veltink, 2013; Trojan et al., 2006). This function is also systematically biased for the fingers – touches on the fingers are consistently mislocalised, more so to neighbouring than to distant fingers (Braun et al., 2011; Braun, Ladda, et al., 2005; Manser-Smith et al., 2018; Schweizer et al., 2001, 2000). Moreover, mislocalisations are not equally likely onto each neighbouring finger, but are biased towards the middle finger (Braun et al., 2011; Manser-Smith et al., 2018; Schweizer et al., 2001).

Despite this pattern of biases being highly consistent across individuals, in a previous study (Manser-Smith et al., 2018) we showed that there are idiosyncrasies in each individual's pattern of tactile confusions across the fingers. Furthermore, we found that these idiosyncrasies are shared across the hairy and glabrous skin surfaces of the fingers (Experiment 2), suggesting that biases arise from a single common

representation of the two skin surfaces, such as in higher-level processing stages where the digits are represented as whole, 3-dimensional units.

As well as comparing tactile biases on the two skin surfaces of the hand, studies have also compared biases in tactile localisation for the fingers of the left and right hands, finding that the overall patterns of localisation are very similar (Schweizer et al., 2001, 2000). This is despite the obvious differences between the two hands, such as that they are mirror reflections of one another, and that for most people hand use is strongly lateralised (Oldfield, 1971). There are also less obvious differences between the left and right hands – for right- and left-handed individuals, as well as ambidextrous people, the right metacarpal bone is larger than the left (Garn, Mayor, & Shaw, 1976; Plato, Woods, & Norris, 1980). In terms of overall hand volume, the dominant hand is generally larger (Kaye & Konz, 1986), but for left-handers the hands are of equal volume (Purves, White, & Andrews, 1994). These differences between right- and left-handed individuals are also reflected in asymmetries in the primary somatosensory cortex (SI) – for right-handers, representations of the right hand are generally larger than for the contralateral hand, though this asymmetry was not found for left-handers (Sörös et al., 1999).

Despite these differences between the structure of the hands and their representations in the somatosensory cortex, there is evidence that representations of touch are highly integrated in both SI and higher cortical areas. One line of evidence comes from behavioural studies, such as those of Tamè and colleagues (2011, 2013), who used double simultaneous stimulation (DSS) to investigate the extent of integration between the left and right hand representations. In this method, tactile stimuli are presented to two digits simultaneously, and reaction times and error rate of responses are

measured in people's ability to detect touch on one of the stimulated fingers. Tamè and colleagues (2011) found that participants respond slower and less accurately when detecting touch applied to non-homologous fingers on the same hand (e.g. left index finger and left middle finger), as well as non-homologous fingers on the *other* hand (e.g. left index finger and right middle finger). This suggests that the representations of the left and right hand are highly integrated, as much as to have a common representation of the two hands.

Other behavioural studies have also indicated that there may be a common representation of the two hands, as various forms of somatosensory information are shared across the hands. For example, when one finger is trained to do a task (such as discriminating tactile orientation, punctuate pressure and surface roughness) tactile learning can be transferred or generalised not only to neighbouring fingers, but to homologous fingers on the other hand (Harrar, Spence, & Makin, 2014; Harris, Harris, & Diamond, 2001). Haggard et al. (2006) found that interweaving the fingers impaired identification of whether a touch was applied to the left or right hand, but not which finger was touched. They suggest that this indicates there is a common representation of the fingers of both hands, with left and right fingers being distinguished only by a secondary process of assigning the fingers to the body representation in external space (Haggard et al., 2006). In individuals with finger agnosia also, it is frequently (but not always) found that finger agnosia is bilateral (Rusconi et al., 2014), indicating reliance on a common finger representation is disrupted.

Evidence from neuroimaging studies have further supported the idea that representations of the left and right hands are highly integrated (for review, see Tamè,

Braun, Holmes, Farnè, & Pavani, 2016). Tamè and colleagues (2012) delivered vibro-tactile stimuli to fingers of the left and right hands and measured responses in SI and SII using fMRI. They found that BOLD responses adapted (became weaker with repeated stimulations) to touches on homologous fingers (even when the fingers were on different hands) in both SI and SII, suggesting that ipsilateral and contralateral signals are integrated in both primary and higher somatosensory processing areas. Using the same paradigm with MEG, Tamè and colleagues (2015) also showed that these areas are involved in different stages of tactile processing – they found response suppression in SI for touches separated by a short interval (25ms), and in SII for touches separated by long intervals (125ms).

Further neuroimaging evidence has suggested that somatosensory information in SI and higher cortical areas may be integrated in the form of bilateral receptive fields (RFs). In macaques, Iwamura and colleagues showed that there are a substantial number of neurons in SI and the upper bank of the intraparietal sulcus with RFs on both hands (Iwamura, 2000; Iwamura et al., 1994). Even for RFs specific to one body side, somatosensory plasticity (i.e. changes in RF size) is linked so that changes to the geometry of RFs in one hemisphere are immediately transferred to the other hemisphere (Calford & Tweedale, 1990). The result of this is the transfer of somatosensory information between digits of the left and right hands, as described earlier (Harrar et al., 2014; Harris et al., 2001).

This study aimed to investigate the similarity of patterns of tactile confusions between the fingers of the left and right hands, and whether there are individual differences in these patterns of confusions that are shared across the two hands. We did

this using testing and analysis methods very similar to our previous studies (Manser-Smith et al., 2018, 2019). If there is a common representation of the two hands that does not distinguish body side, as Tamè et al. (2011; 2013) suggest, we would expect to find shared idiosyncratic differences in patterns of tactile confusions between the left and right hands. All procedures, including sample size, exclusion criteria, and analysis plans were pre-registered on the Open Science Framework (OSF; osf.io/msb6d).

4.2. Methods

Participants

In our previous studies using this paradigm (Manser-Smith et al., 2018, 2019), the t-test assessing individual differences found between the two surfaces of the fingers had a Cohen's *d* of 1.04. We based our calculations on a one-tailed t-test, as we have a clear directional prediction that classification accuracy should be greater than chance level, rather than lower than chance. As such, we conducted a power analysis using G*Power 3.1 (Faul et al., 2007) Cohen's *d* of 1.04, an alpha value of 0.05, and power of 0.90, which indicated that 10 participants were required.

To remain consistent with previous experiments, we recruited 20 participants (11 female; mean age = 29.35 years, SD = 11.00). All 20 participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971); mean = 64.50, range = 10 – 100). All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

Stimuli

As in our previous experiment, tactile stimuli were applied to the fingers using a von Frey hair. As the fingers have a small point localisation threshold and pressure sensitivity threshold (Schweizer et al., 2000), individuals can very accurately localise touch to the individual fingers when using an above-threshold stimulus. As such, we used a procedure adapted from our previous studies at the beginning of each experiment, to determine the weakest strength von Frey hair that the participant could consistently detect while still making a sufficient number of mistakes (mislocalisations) for us to measure patterns of confusion between fingers. The results of our previous study (Manser-Smith et al., 2018) and other studies (Duncan & Boynton, 2007; Sathian & Zangaladze, 1996; Vega-Bermudez & Johnson, 2001) showed that tactile sensitivity decreases from the thumb to the little finger. As such, we only tested the little finger in this procedure, as the weakest strength of von Frey hair detectable by the little finger should also be detectable on the other fingers. We carried out this procedure separately on the two hands, as previous research suggests that tactile sensitivity may differ across the two hands (Weinstein & Sersen, 1961).

Five strengths of von Frey hair were tested, from 0.008g (1.65) to 0.16g (3.22). These were the five weakest strengths of von Frey hair available to us. During pilot testing and in previous experiments (Manser-Smith et al., 2018, 2019) we found that a large number of participants could identify even the weakest strength von Frey hair used, although we still tested a wider range of five stimuli strengths to ensure that we found the correct threshold for each participant. Participants received tactile stimulation on the hairy skin of the little finger of the left or right hand, by each strength von Frey

hair, starting from the weakest strength. Once the little finger was tested with the strongest von Frey hair the procedure was reversed, reducing the strength of the von Frey hair to the weakest again. This staircase was carried out twice, and the average number of correct responses was calculated for each strength of von Frey hair. The weakest strength von Frey hair used by which participants could correctly localise above 70% of touches was chosen for use in the experiment. This threshold was chosen as it is greater than chance performance, but still provides mislocalisations for us to measure. The mean strength von Frey hair used on the right hand was 2.38g (range = 1.65 – 2.44g), and the left hand 2.37g (range = 1.65 – 2.44g). The strength of von Frey hair used for each participant was strongly correlated across the two hands, $r(17) = 0.72$, $p < 0.001$. A paired-samples t-test confirmed that strengths of von Frey hair used were not significantly different between the two hands, $t(19) = -0.36$, $p = 0.72$, $d = -0.08$.

Task

The procedures closely followed those used in our previous study and did not deviate from our preregistered plans. Participants were seated in a comfortable position with their left and right hands resting palm-down on a table. This posture was kept consistent regardless of whether the left or right hand was being tested, and they were instructed to remain as still as possible throughout each experimental block. The experimenter used a von Frey hair to apply tactile stimulation to the medial phalange of the dorsal surface of the participant's finger for around 500ms. One finger was stimulated per trial. Participants were asked to respond by verbally identifying which

digit they felt had been stimulated. Digits were identified by numbers 1 to 5: the thumb corresponding to number 1, to the little finger corresponding to number 5.

There were four experimental blocks, two in which the fingers of the left hand were stimulated, and two in which the fingers of the right hand were stimulated. Stimulation was only applied to the hairy skin, and not on the glabrous skin. The hairy skin was chosen because in our previous experiment (Manser-Smith et al., 2018) participants reported it to be more comfortable to sit in the position where the hairy skin can be tested (i.e. with the hands palm down), and because tactile sensitivity thresholds were more consistent over the hairy skin of the fingers, meaning it was easier to select an appropriate von Frey hair. ABBA counterbalancing was used to vary order of presentation, with the first condition counterbalanced across participants. Each block contained 100 trials, 20 for each of the 5 digits. The order of digit stimulation was pseudo-randomised within each block of trials, so that there was an approximately equal number of each type of preceding trial.

Figure 4.1. Experimental set-up. The participant sat in a chair with both their hands resting palm-down on a table in front of them at an equal distance from the body midline. Vision of the hands was prevented using a piece of black cardboard.

Analysis

The analyses closely followed our previous study and our preregistered plans. Two confusion matrices were obtained per participant, one showing the pattern of mislocalisations on the hairy skin of the fingers of the left hand, and the other showing the pattern of mislocalisations on the right hand. Each confusion matrix is a 5x5 grid where each column represents stimuli applied to one digit, and each row represents the proportion of trials on which the participant judged that one digit was touched. As such, the confusion matrix nicely shows the proportion of correct localisations, as well as the direction and magnitude of bias for mislocalisations.

A directionality index (DI) was calculated in order to give a single value to indicate both direction and magnitude of bias in finger selection, as in our previous study (Manser-Smith et al., 2018) and that of Cicmil et al. (2016). For each finger, the

mean of the responses given to identify which finger was stimulated was calculated, minus the actual finger number of the stimulated finger:

DI = (mean of response finger numbers - stimulated finger number).

Initially, we attempted to replicate the pattern of directional biases found on the hairy skin of the fingers in our previous study. To do this we carried out one-sample t-tests comparing the DI score of the central three digits of the left and right hand to zero. We also carried out a repeated-measures ANOVA with two factors: Stimulated Digit (1 to 5) and Hand (left/right), and percent accuracy as the dependent variable. A Bayesian repeated-measures ANOVA was also carried out with the same factors and dependent variable, in order to assess whether the null hypothesis (H_0) should be accepted over the alternative hypothesis (H_1). This was done using the default parameters in JASP 0.8.2.0 (Wetzels et al., 2012).

The central question of this study concerns whether there are shared individual differences in the pattern of mislocalisation on the two hands. To address this we used representational similarity analysis (RSA; Kriegeskorte, Mur, & Bandettini, 2008) to assess the overall pattern of the confusion matrices on the two hands, analogous to the procedure we used in our previous work to compare the two sides of the feet and hands (Manser-Smith et al., 2018). Specifically, we used a leave-one-participant-out procedure in which we regressed the 20 off-diagonal cells (i.e., the localisation errors) of each participant's confusion matrix on the grand average confusion matrix for the other 19 participants. The resulting residuals quantify the way in which a given participant's

confusion matrix differs idiosyncratically from the pattern shown by the other participants. Critically, this procedure eliminates differences between participants in overall levels of accuracy, isolating the pattern of confusions between digits, rather than overall performance. These residuals were calculated separately for the confusion matrices on the left and right hand, resulting in two sets of residuals per participant.

If there are shared individual differences between the fingers of the left and right hand, the two sets of residuals for a given participant should be similar. That is, a participant who differs idiosyncratically from other people on the fingers of the left hand should also differ in the same way on the right hand. To assess this, we used a cross-correlation classification procedure. For each participant, we calculated the correlation between the two patterns of residuals, the within-participant cross-correlation. Then we calculated the 38 cross-correlations comparing each of that participant's two patterns to the opposite pattern of each of the other 19 participants. Classification accuracy was calculated for each participant as the percentage of those 38 between-participant correlations which were smaller than the within-participant cross-correlation. A one-sample t-test was used to assess whether classification accuracy is significantly greater than chance (i.e. 50%). We used a one-tailed test given that we had a clear directional prediction that classification accuracy would be above chance. We also carried out a Bayesian one-sample t-test in order to assess whether the null hypothesis (H_0) should be accepted over the alternative hypothesis (H_1). This was done using the default parameters in JASP 0.8.2.0.

The raw data from this research are freely available through the OSF (osf.io/bm253).

4.3. Results

Directional Bias for Localisation of the Fingers

Figure 4.2 (left panel) shows the confusion matrix for tactile localisation on the fingers of the left hand. As in our previous studies (Manser-Smith et al., 2018, 2019), finger identification errors were not randomly distributed, but were biased towards the centre of the hand. Analysis of the DI results showed that mislocalisation of touches to the index finger was biased towards the little finger (*M*: 0.27, SD: 0.17), $t(19) = 6.93$, $p < 0.0001$, $d = 1.59$, the ring finger was biased towards the thumb (*M*: -0.33, SD: 0.20), $t(19) = -7.06$, $p < 0.0001$, $d = -1.65$, and the middle finger was not biased in either direction (*M*: 0.00, SD: 0.12), $t(19) = 0.05$, $p = 0.96$, $d = 0.00$. These results provide a direct replication of the results of our previous study, both in the direction and magnitude of localisation biases for each of the central three fingers of the hand (Manser-Smith et al., 2018, 2019), as well as previous studies of finger localisation (Braun et al., 2011; Braun, Ladda, et al., 2005; Schweizer et al., 2001, 2000).

Figure 4.2 (right panel) shows the confusion matrix for tactile localisation on the fingers of the right hand. As for the left hand, finger identification was biased towards the centre of the hand. The index finger was biased towards the little finger (*M*: 0.27, SD: 0.17), $t(19) = 6.93$, $p < 0.0001$, $d = 1.59$, the ring finger was biased towards the thumb (*M*: -0.33, SD: 0.20), $t(19) = -7.06$, $p < 0.0001$, $d = -1.65$, and the middle finger was not biased in either direction (*M*: 0.00, SD: 0.12), $t(19) = 0.05$, $p = 0.96$, $d = 0.00$.

Paired-samples t-tests confirmed that DI was not significantly different between the left and right index, middle or ring fingers (all $p > 0.05$). These results show that

directional biases in tactile localisation of the hairy skin of the fingers are highly consistent across the left and right hands at the group level.

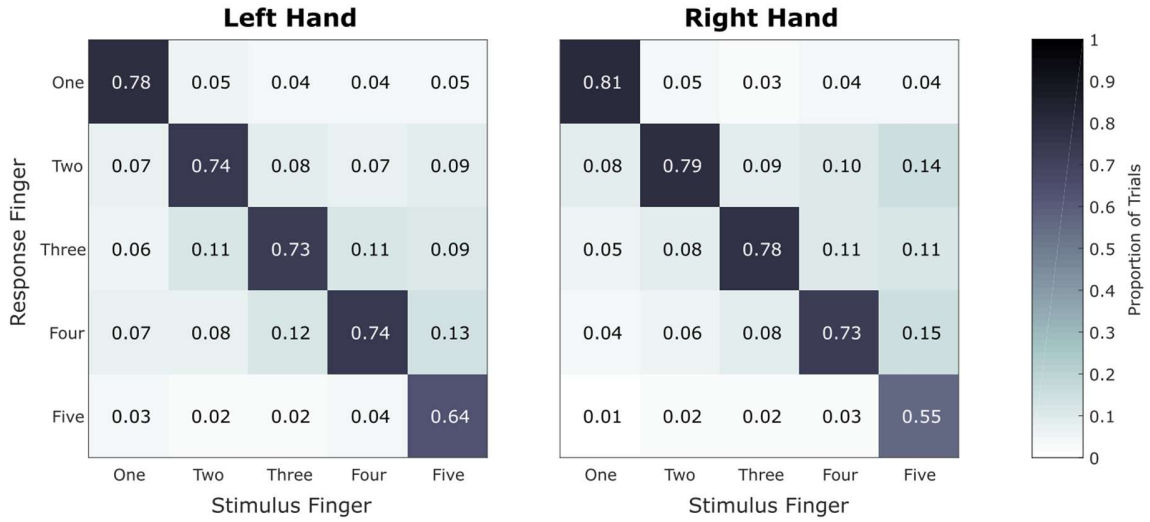

Figure 4.2. Confusion matrices showing the proportion of stimuli judged as located on each of the five fingers as a function of which finger was actually stimulated. Fingers were identified by numbers one (thumb) through five (little finger). Data from the left hand is shown in the left panel, and from the right hand in the right panel. The proportion of correct responses for each finger is shown along the diagonal from the top-left to the bottom-right. The off-diagonal cells represent mislocalisations between the fingers.

Response Accuracy for Localisation of the Fingers

The results of the repeated-measures ANOVA indicated that accuracy was significantly different depending on which digit was stimulated ($F(4,76) = 13.89$, $p < 0.001$, $\eta_p^2 = 0.42$). Bonferroni-corrected paired-samples t-tests indicated that localisation accuracy was significantly lower on the little fingers than all other digits ($p < 0.001$) but was not different between any of the other digits. This result again provides a direct replication of previous findings on the hairy skin of the fingers (Braun et al., 2011; Braun, Ladda, et al., 2005; Manser-Smith et al., 2018, 2019; Schweizer et al., 2001,

2000), that localisation accuracy decreases from the thumb to the little finger, dropping off significantly for the little finger.

The results of the ANOVA also showed that localisation accuracy did not differ significantly between the two hands ($F(1,19) = 0.23$, $p = 0.64$, $\eta_p^2 = 0.01$), and that there was no significant interaction between Stimulated Digit and Hand ($F(4,76) = 2.08$, $p = 0.09$, $\eta_p^2 = 0.10$). A Bayesian repeated-measures ANOVA provided moderate evidence in support of the null against the alternative hypothesis for the effect of hand ($BF_{01} = 6.19$), but only weak evidence for the null hypothesis for the interaction ($BF_{01} = 1.58$).

Shared Individual Differences Between the Fingers of the Left and Right Hands

The most intriguing question of this study is whether individual differences in the pattern of mislocalisations is shared between the fingers of the left and right hands. We calculated the residual differences between each participant's pattern of mislocalisations and the average pattern of mislocalisations of all other participants (separately for the left and right hands). We then calculated the correlation between residuals of the participant's own left and right hands (within-participant correlation), and the correlation between residuals of the participant's left and right hand, and the left and right hand residuals from the remaining participants (between-participant correlation). We classified the correlation coefficients according to whether they were greater for within- or between-participant comparisons, so that higher classification accuracy indicates participant's responses on one hand were more similar to their own responses on their other hand than to responses of all other participants.

On average, classification accuracy was 67.89%, which was significantly above chance (i.e. 50%), $t(19) = 2.81$, $p = 0.01$, $d = 0.63$. This indicates that a greater than chance number of idiosyncrasies in each participant's pattern of mislocalisations were shared between the left and right hands of the individual participant than between the individual and *other* participants' patterns. In other words, individual differences in each participant's responses were more similar across the left and right hands of the participant than to other participant's hands. A Bayesian one-sample t-test provided very strong evidence in support of the alternative hypothesis against the null hypothesis, $BF_{10} = 9.27$. Across participants, classification accuracy ranged from 2% to 100%, but exceeded 50% in 15 out of 20 participants.

4.4. Discussion

In this study we investigated the patterns of confusions for localisation of tactile stimuli across the fingers of the left and right hands. We replicated the highly consistent patterns of confusions found across the fingers in previous studies (Braun et al., 2011; Braun, Ladda, et al., 2005; Manser-Smith et al., 2018; Schweizer et al., 2001, 2000), and again demonstrated that this pattern of tactile confusions is highly consistent across the left and right hands (Schweizer et al., 2001, 2000). We also found that despite this highly consistent pattern of mislocalisations, there are idiosyncratic differences in participants' performance that were shared between the left and right hands, such as has been previously found to be shared across the hairy and glabrous skin surfaces of the fingers (Manser-Smith et al., 2018).

The finding of shared idiosyncrasies between the two hands provides further evidence that somatosensory representations of the body are highly integrated in SI and higher-cortical areas, as suggested previously by behavioural and neuroimaging evidence (e.g. Tamè et al., 2011, 2012, 2013, 2015, 2016). Furthermore, this result supports the hypothesis that there is a single, common representation of both the left and right hands (Tamè et al., 2011). Tamè and colleagues do not define the representational stage at which they believe this may occur (Tamè et al., 2011), but in previous studies using this paradigm we have suggested that mislocalisations may arise from higher-order representations of the body (Manser-Smith et al., 2018, 2019). There is already evidence for a single representation of the two hands in higher-order representations of the body, for example from Tamè and colleagues' fMRI (2012) and MEG (2015) experiments, as well as findings RFs on the bilateral hands in SI and higher-cortical areas of macaques (Iwamura, 2000; Iwamura et al., 1994).

In contrast to previous studies (Schweizer et al., 2001, 2000) that reported increased tactile sensitivity on the left hand, compared to the right, we found that response accuracy was no different across the two hands. All participants in the present study, like those in Schweizer and colleagues' studies, were right-handed, suggesting that the contradictory findings of these studies are not a result of differences in tactile acuity across the two hands, dependent on hand-dominance. Moreover, the findings of our experiment are consistent with previously reported results from Weinstein (1968), that despite differences in pressure sensitivity across the two hands, there was no difference in performance on a point localisation task (such as performed in the present study).

From the results of the present experiment, and our previous two experiments using this paradigm (Manser-Smith et al., 2018, 2019), it seems that reliance on a common representation of two body parts may differ depending on the body parts used in a particular task. As we used the same exact paradigm in each of our experiments, we can directly compare the classification accuracy scores across them. By comparing classification accuracy across each of our experiments we can see which body parts share the most individual differences in performance, as higher classification accuracy indicates more similarities shared across the two body parts compared. The most idiosyncrasies in performance are shared across the two skin surfaces of the toes (82.37%; Manser-Smith et al., 2018). A large number of idiosyncrasies in performance are also shared across the two skin surfaces of the fingers (74.61%; Manser-Smith et al., 2018). Fewer idiosyncrasies in performance are shared across the left and right hands (67.89%), and least similarities in performance are shared between the hands and feet (59.25%; (Manser-Smith et al., 2019). An independent-samples ANOVA showed that there was a significant difference between classification for each of these body part comparisons, $F(3,96) = 4.43$, $p < 0.01$, $\eta_p^2 = 0.12$, although Bonferroni-corrected paired-samples t-tests showed that only the strongest classification accuracy (between the two skin surfaces of the toes) and the weakest (between the fingers and toes) were significantly different from one another, $t(58) = 3.44$, $p < 0.01$, $d = 0.99$. This comparison across our four studies is a measure of the degree that representations are shared between the body parts compared. Representations of the two skin surfaces of the toes and fingers are shared to the greatest extent – as they are on alternate sides of the same body parts they are both physically similar, and intrinsically 'joined' together in

the movement of the body part. The representation of the left and right hands is shared to a lesser degree than the hand and foot representations, as although they are physically similar mirror images of one another, their movements are not intrinsically joined. The representation of the hand and foot is shared of the representations described, as not only are the physical differences between the hand and foot the most distinct, so are the movements of these two body parts.

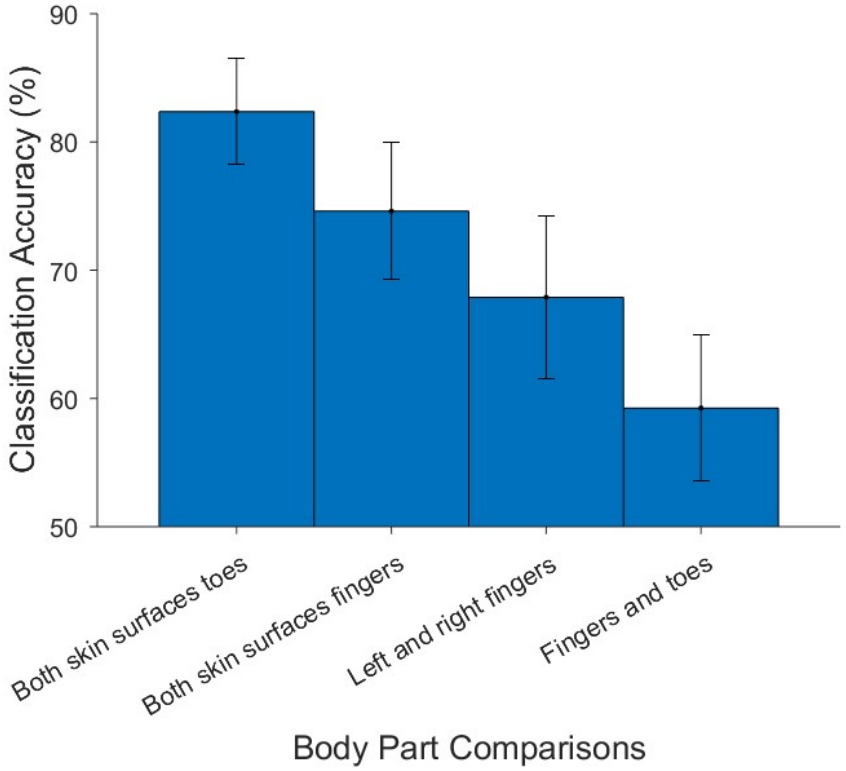

Figure 4.3. Graph comparing classification accuracy across the four experiments conducted by ourselves using the same experimental paradigm. The graph shows that classification accuracy was highest between the two skin surfaces of the toes, indicating that individual participants shared the greatest amount of similarity in mislocalisation pattern across these two skin surfaces. Participants shared the least amount of similarity in idiosyncrasies of mislocalisation pattern between the fingers and toes.

In the present experiment, we showed that patterns of tactile confusions are highly consistent across the left and right hands. Although this pattern is highly consistent across the two hands, and across participants, we can identify individual differences in response patterns that are shared across the fingers of the left and right hands. This finding supports the hypothesis previously put forward by Tamè et al. (2011), that there is a common representation of the left and right hands.

Chapter 5: Tactile localisation on the two skin surfaces of the hands and feet

5.1. Introduction

There is a large body of research investigating our ability to localise touch on the body, specifically on the hands, much of it describing the systematic biases that occur in our ability to do so. For example, touches on the fingers are more frequently mislocalised to neighbouring rather than distant digits, with mislocalisations biased towards the middle finger of the hand (Manser-Smith et al., 2018; Schweizer et al., 2000). When localising touch on the continuous skin surface of the hand dorsum (as opposed to discreet body parts such as the digits) people show consistent distal and radial biases in localising points on the hairy skin surface of the hand, with magnitude of biases being strongest closer to the wrist than the digits (Mancini et al., 2011; Margolis & Longo, 2014). These biases differ on the glabrous skin surface of the hand – a weaker and less consistent proximal bias in localisation is found on this skin surface (Culver, 1970; Mancini et al., 2011).

Finding different patterns and magnitudes of mislocalisation across the two skin surfaces of the hand can give some insight into the origin of localisation biases. Mancini and colleagues suggest that low-level somatosensory processing may play a role specifically in the *magnitude* of biases found. Firstly, the glabrous skin surface is more densely innervated with mechanoreceptors than the hairy skin surface (Ackerley et al., 2014; Provitera et al., 2007) resulting in smaller biases on this skin surface. Moreover, for the hairy skin surface of the hand, receptive fields (RFs) of primary tactile neurons innervating this skin surface are anisotropic and oval-shaped, with the long axis running

proximo-distally (Alloway et al., 1989; Brooks et al., 1961; Brown et al., 1975). For the glabrous skin surface of the hand, however, RFs of primary neurons are generally smaller and less elongated (DiCarlo & Johnson, 2002; DiCarlo et al., 1998). While it is clear that this may lead to a reduction in variable error (precision of localisation) on the glabrous skin surface compared to the hairy skin (Margolis & Longo, 2014; Medina et al., 2018; Sadibolova, Tamè, Walsh, & Longo, 2018), it is not clear how this may lead to a systematic pattern of constant error (Mancini et al., 2011).

Mancini et al. (2011) also suggest that higher-order somatosensory processing may contribute to the biases in tactile localisation found on the two skin surfaces, specifically in the *direction* of biases. They carried out a localisation task using a laser stimulus that caused pinprick pain and non-painful heat (as opposed to innocuous touch), so they could stimulate different afferent fibres in the skin surface. They found that patterns of tactile biases using these stimulation methods were consistent with those described in the previous paragraph when using innocuous touch, suggesting that differences in bias direction are not attributable to low-level somatosensory processing. However, in higher-order somatosensory processing at the primary somatosensory cortex (SI) the hairy and glabrous skin surfaces of the hand are represented in two distinct maps (Merzenich et al., 1978; Nelson et al., 1980). So, different patterns of localisation biases on the hairy and glabrous skin surfaces may arise from their distinct representations in SI.

To our knowledge, it has not been tested if there are biases in tactile localisation (like those found by Mancini et al. [2011] on the hand) on the hairy and glabrous skin surfaces of the feet. The feet also have hairy and glabrous skin surfaces on their alternate

sides (Marieb, 2012), as well as sharing an overall similar structure to the hands (Owen, 1849/2008), as a result of their co-development throughout human evolution (Rolian et al., 2010). On a psychological level, the literature suggests that there are strong connections between somatosensory representations of the hands and feet. I previously mentioned finger agnosia, a symptom of Gerstmann's syndrome (Kinsbourne & Warrington, 1962), for which toe agnosia is also a common co-occurring symptom (Mayer et al., 1999; Tucha et al., 1997). The stereotypical pattern of tactile confusions described above for the fingers (Manser-Smith et al., 2018, 2019; Schweizer et al., 2000), is also similar for the toes (Cicmil et al., 2016; Manser-Smith et al., 2018, 2019). Moreover, there is evidence to suggest that there is a single common somatosensory representation of the hands and feet – idiosyncrasies in individual patterns of digit mislocalisation are shared across the fingers and toes, suggesting they arise from a common, high-level representation of the two body parts (Manser-Smith et al., 2019).

Yet there are also differences between the hands and feet, for example, the obvious and dramatic difference in how we use our hands and feet during our everyday lives, as well as their differences in size and shape (Marieb, 2012). One less obvious difference between the hands and feet is the different mechanoreceptor types and activation thresholds – the glabrous skin surface of the foot has fewer slow-adapting mechanoreceptors than the glabrous skin of the hand (Kennedy & Inglis, 2002). Moreover, both slow-adapting and fast-adapting type 1 receptors had a much higher activation threshold on the foot than on the hand (Kennedy & Inglis, 2002), perhaps reflecting their different usage patterns. On the hairy skin surface, the fingers again have low pressure sensitivity thresholds compared to the toes (Schweizer et al., 2000), and as

such localisation of near-threshold stimuli is more accurate on the fingers than the toes (Cicmil et al., 2016; Manser-Smith et al., 2019).

The aim of this study is to investigate whether there are similar biases in tactile localisation on the feet, as on the hands, as well as whether tactile localisation differs across the hairy and glabrous skin surfaces of the feet in the same way as across the two skin surfaces of the hands. We will do this using testing and analysis methods very similar to those used by Mancini et al. (2011). If the patterns of tactile mislocalisation are similar across the two skin surfaces of both the hands and feet, this may suggest that the patterns of mislocalisations are a general feature of the limbs, or further, provide additional evidence that there is a common representation of the hands and feet.

5.2. Methods

Subjects

Twenty individuals participated in the experiment. One participant was excluded from the analysis for not following task instructions – the majority of responses made were far outside of the hand silhouette. As such, 19 participants' data were analysed (15 female, mean age = 28 years, range = 20 - 67). Participants all had normal or corrected-to-normal vision and normal touch. All 19 participants were right-hand dominant, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean = 71; range = 42 - 100), and right-foot dominant, as assessed by the Waterloo Footedness Questionnaire (Elias & Bryden, 1998; mean = 50; range = 20 – 100). EHI and WFQ scores were correlated across participants ($r = 0.60$, $p < 0.01$). All participants gave

written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological ethics committee.

The main effect of interest from the study by Mancini and colleagues (2011) was the distal component of bias on the hairy skin surface of the hand. Cohen's *d* values for this effect from the three experiments reported by Mancini et al. (2011) were 2.05, 1.75 and 1.68, respectively. A power analysis using G*Power 3.1 (Faul, Erdfelder, Buchner, & Lang, 2007) with the smallest of these effect sizes, an alpha value of 0.05, and power of 0.95, indicated 7 participants were required. As such, with 19 participants, our experiment is well powered to extend the results of Mancini and colleagues to the feet.

Apparatus and stimuli

The experimental paradigm was closely modelled on several previous studies investigating tactile localisation on the hand (Longo, Mancini, et al., 2015; Mancini et al., 2011; Margolis & Longo, 2014). The experimental set-up is shown in Figure 5.1. Participants were asked to sit at a desk with a computer screen around 30cm in front of them. To their left was an arm rest on which they rested their left arm during the entirety of the experiment. While the experimenter was testing the hand the participant held their hand with fingers pointing upwards so that the both the top and bottom surfaces of the hand were easily accessible to the experimenter. While the hand was not being tested the participant lay it down flat on the arm rest. Vision of the hand was occluded using a piece of black cardboard between the screen and the arm rest (height: 40cm). The participant rested their bare left foot on a stool (height: 40cm) underneath the desk, with toes pointing upwards so that the top and bottom of the foot could be seen. The tactile

stimulus was applied using a von Frey hair of weight 26g, as this was strong enough to be suprathreshold in all participants without causing discomfort.

Information about the current trial was presented to the experimenter on a monitor by a custom MATLAB script (Mathworks, Natick, MA), but was not visible to the participant. On each trial the participant saw a fixation cross on the screen while the experimenter was applying the tactile stimuli. Roughly one second after the stimulus was applied, the participant saw a silhouette of either their own foot or hand (depending on the block), and used the mouse cursor (a '+') to select the location where they perceived the touch. The starting location of the cursor on the screen was randomised for each trial. Participants' vision of their hand holding the mouse was also occluded by a piece of black cardboard.

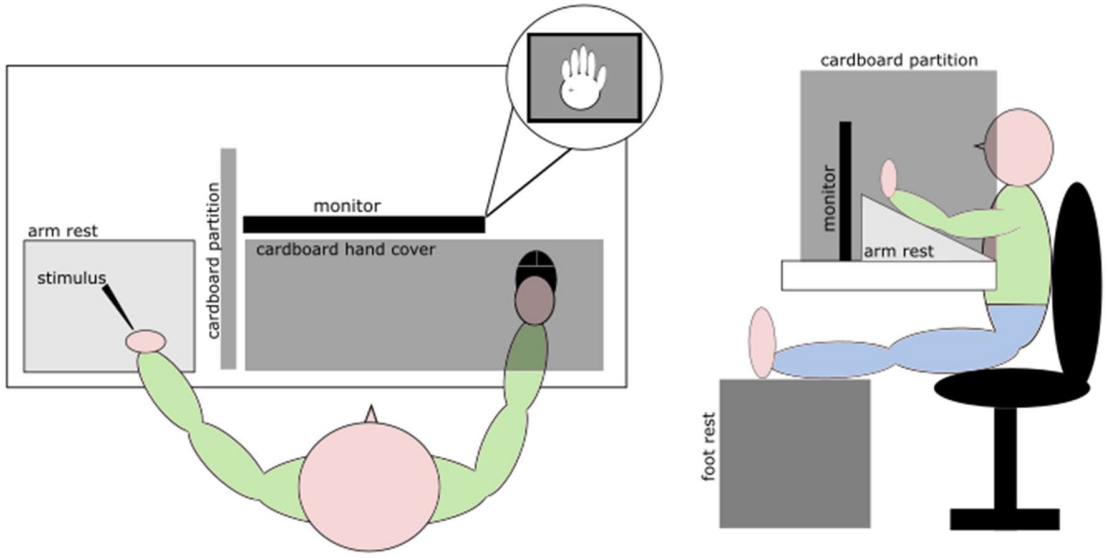

Figure 5.1. Experimental set-up. Participants sat on a chair in front of a computer screen on a desk. A mouse was positioned in front of the computer screen, but vision of the hand using the mouse was obscured by a piece of black cardboard level with the bottom of the computer screen. The left foot was resting on a stool underneath the desk, and the left hand was resting on an arm rest. Vision of the foot was obscured by the desk, and vision of the hand was obscured by another piece of black cardboard between the participant and the arm rest.

Procedure

On arriving to complete the experiment, participants were evaluated on their hand and foot dominance using the Edinburgh Handedness Inventory (Oldfield, 1971) and the Waterloo Footedness Questionnaire (Elias & Bryden, 1998). All participants were tested on their left hand and foot. The experimenter marked a three-by-three point grid on both sides of the hand and foot, as a guide for applying the tactile stimuli. Each point was separated by 2cm, so the grid extended 6cm along and 6cm across the hand. Photos were taken of the grids on both sides of the hands and foot for analysis, using the experimenter's mobile phone camera (HTC 10; resolution: 12 MP). Photos were taken approximately 30 cm from the surface of the hand and foot, and the camera was held level with the body part – this was particularly important on the hairy surface of the foot, which slopes from the ankle to the toes. Photos also included a 30 cm ruler held level with the surface of the hand or foot. The experimenter edited the pictures of the top of the foot and top of the hand using GNU Image Manipulation Program (GIMP version 2.8.2) to create the silhouettes presented to the participant during the experiment. Participants were instructed not to look at their hand or foot once the grid was marked, and to keep their position as still as possible throughout the experimental blocks.

Once the participant was seated in front of the computer with their hand and foot in comfortable positions, they were instructed to fixate on the cross on the screen. On each trial the experimenter used a von Frey hair to apply tactile stimulation to one of the nine points on the hand or foot for around 500ms. Participants were asked to respond quickly and accurately, by moving the cursor within the silhouette to the location where they perceived the touch. Importantly, the orientation of the hand or foot silhouette

displayed to the participants did not change whether the hairy or glabrous skin was stimulated. Unlike the hand, the foot cannot be easily rotated to view either skin surface, so when stimulating the two skin surfaces of the foot it must be kept in a constant position. As such, we did not change the orientation of the foot silhouette as the orientation of the foot did not change. We also did not change the orientation of the hand to remain consistent across conditions, a difference between this study and that of Mancini and colleagues (2011). When the glabrous skin was stimulated, participants were required to localise the point of tactile stimulation as if they were looking *through* the hand or foot. Despite this, results are presented so that it appears that you are looking *directly at* the stimulated skin surfaces.

Participants generally responded around one or two seconds after stimulation, so that overall stimulation was applied at a rate of roughly 15 to 20 trials per minute. As such the experiment took between 45 minutes and one hour to complete. There were eight experimental blocks – two for each side of the hand and foot. The participants completed the four block types (hairy skin of the hand, glabrous skin of the hand, hairy skin of the foot, glabrous skin of the foot) in a random order, then again in the reverse order. There were a total of 45 trials per block, five repetitions of each of the nine locations. Each block was divided into five smaller blocks, each consisting of one trial of each location in random order. Between each block participants were allowed a break.

Analysis

The analysis carried out was also closely modelled on Mancini et al. (2011). To place the actual location of each landmark (on the hand) and the judged location (on the computer screen) into a common reference frame, we used the two-point registration method developed by Bookstein (1991) (Bookstein coordinates). Two specified landmarks are defined as being points (0,0) and (1,0) with other landmarks positioned accordingly. On both skin surfaces of the hand, we defined the outer edge of the base of little finger as point (0,0) and the outer edge of the base of the index finger as point (1,0). On both skin surfaces of the foot, we defined the outermost edge of the base of the little toe as point (0,0) and the outermost edge at the base of the big toe as point (1,0).

At the start of testing each participant, pictures were taken of the two skin surfaces of the hand and foot, with the grid of stimulus locations marked. The stimulated locations were calculated in *x* and *y* pixel coordinates from the photos, for each skin surface and body part, and the participants' estimates of stimulus locations were calculated in *x* and *y* pixel coordinates on the computer screen. For the two skin surfaces of the hands, the locations of the outer edge of the base of the index and little finger were measured in *x* and *y* pixel coordinates. On the two skin surfaces of the feet, the locations of the outermost edge at the base of the big toe and little toe were also measured in *x* and *y* pixel coordinates. Using this procedure is important firstly, as it places the locations of the stimuli (coded from a photograph of each participant's hand) and the locations of the responses (defined by mouse clicks on the computer screen) into a common reference frame for comparison. Secondly, it defines unit length relative to the size of each participant's hand, removing individual differences in overall hand size,

allowing averaging across participants. Finally, using Bookstein coordinates orients the error vectors so that the *x*-coordinate is aligned with the radio-ulnar axis of the hand/foot, and the *y*-coordinate with the proximo-distal axis, allowing us to isolate radial and distal components of error vectors.

In order to directly compare biases in localisation across the hand and the foot in the second part of our analyses, we converted biases in Bookstein units into centimetres (cm). Due to morphological differences between the hand and the foot, and the different landmarks used to calculate Bookstein units on the two body parts, the scale of the Bookstein units is not directly comparable between the two body parts. We calculated number of cm between the two landmarks used to define the Bookstein coordinates for each participant, on the two skin surfaces of each body part. For each participant, we multiplied their responses in Bookstein units by this value to measure their responses in cm.

Two independent components of localisation error were calculated, constant error and variable error. Constant error (CE) is the average error calculated from multiple localisation attempts, and is a measure of overall bias in localisation for each point. We analysed CE separately in terms of its distal and radial components. Variable error is the standard deviation of multiple responses, and a measure of the precision of localisation. Again, this was analysed in terms of its distal and radial components.

5.3. Results and discussion

Tactile localisation on the hand

The left panel of Figure 5.2 shows the average position of actual and judged locations on the *hairy* skin of the hand. There was a significant distal component of the grand average CE vector ($t(18) = 37.82$, $p < 0.001$, $d = 8.68$), which was on average biased by 0.53 Bookstein units (± 0.01 [SE]). Distal components of each point's CE vector differed significantly across the nine locations on the hairy skin of the hand ($F(8,144) = 50.88$, $p < 0.001$, $\eta_p^2 = 0.74$). Bonferroni-corrected post-hoc comparisons confirmed that distal bias increased from the left to the right side of the hand (towards the thumb), as each column of locations was significantly different from one another (all $p < 0.001$). Distal bias was also greater for points closest to the knuckles, as this row was significantly different from the middle row and the bottom row of points (both $p < 0.05$), although the middle and bottom rows were not significantly different from one another ($p = 0.30$). This replicates one of the main findings of Mancini et al. (2011), that there are significant distal biases in localisation on the hairy skin surface of the hand, although they report stronger biases for points closer to the wrist, not the knuckles and thumb as we found.

There was also a significant radial component of the grand average CE vector ($t(18) = 8.24$, $p < 0.001$, $d = 1.89$), on average biased by 0.06 Bookstein units (± 0.01). Radial components of the CE vector across the nine locations also varied, but to a lesser extent ($F(8,144) = 3.62$, $p < 0.001$, $\eta_p^2 = 0.17$). Bonferroni-corrected post-hoc comparisons showed that radial bias was greater for points closest to the knuckles, as this row was significantly different from the middle row and the bottom row of points

(both $p < 0.05$), although the middle and bottom rows were not significantly different from one another ($p = 0.85$). This replicates another one of the main findings of Mancini et al. (2011), that there are significant radial biases on the hairy skin surface of the hand, and magnitude of radial biases are smaller than distal biases.

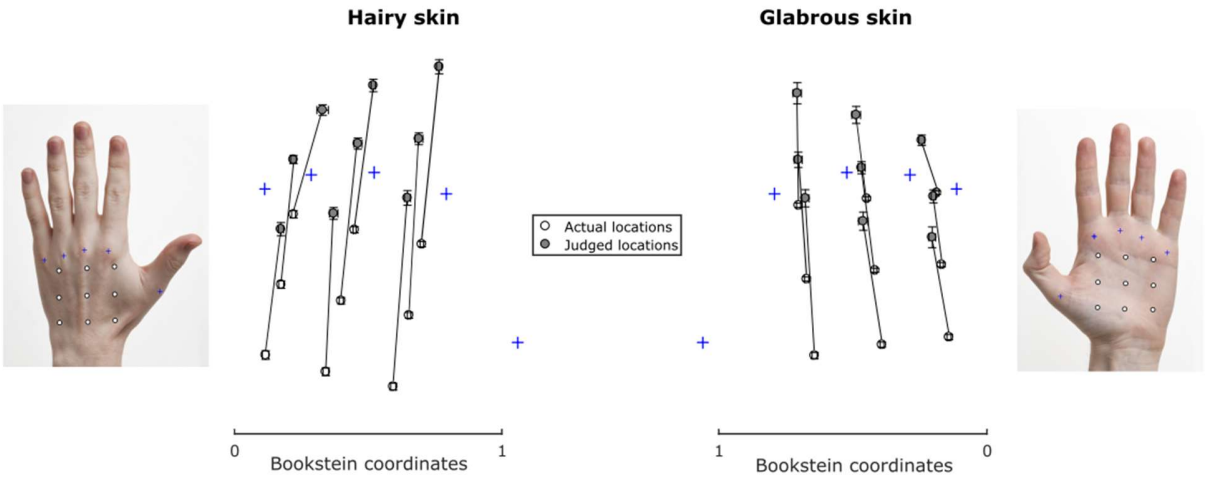

Figure 5.2. Perceptual map of touch on the hairy skin (left) and glabrous skin (right) of the left hand. The average actual (white circles) and judged (grey circles) locations of the nine stimulated points on the hand are plotted in Bookstein coordinates, centred on the outer edge of the little finger (0,0) and the index finger (1,0). Although the hand was not turned during testing, the data is presented as though it was, looking *directly at* the stimulated skin surface. As such, the thumb is located to the *right* of all points on the hairy skin, and the *left* of all points on the glabrous skin. Blue crosses indicate the locations of the knuckles of each finger. Error bars represent SE.

The right panel of Figure 5.2 shows the average position of actual and judged points on the *glabrous* skin of the hand. There was a significant distal component of the grand average CE vector ($t(18) = 20.86$, $p < 0.001$, $d = 4.79$), on average biased by 0.36 Bookstein units (± 0.02). CE vectors of the nine dorsum locations on the glabrous skin differed significantly in terms of their distal components ($F(8,144) = 20.86$, $p < 0.001$, $\eta_p^2 = 0.54$). Bonferroni-corrected post-hoc comparisons showed that distal bias

increased towards the thumb, as each column of locations was significantly different from each other (all $p < 0.001$). Distal bias was also greater for points closest to the wrist, as this row was significantly different from the middle row and the top row of points (both $p < 0.05$), although the top and middle rows were not significantly different from one another ($p = 0.08$).

There was also a significant radial component of the grand average CE vector ($t(18) = 6.56$, $p < 0.001$, $d = 1.51$), on average biased by 0.04 Bookstein units (± 0.01). Radial components of the CE vector varied across the nine locations on the glabrous skin of the hand ($F(8,144) = 2.77$, $p < 0.05$, $\eta_p^2 = 0.13$), with biases tending to be greater towards the wrist. Bonferroni-corrected post-hoc comparisons showed that the row of points closest to the wrist was significantly different from the middle row ($p < 0.01$), although no other comparisons were significant (all $p > 0.05$).

We further investigated similarities in responses across the two skin surfaces, first by correlating distal and radial components of grand average CE vector across the hairy and glabrous skin surfaces. While distal components of CE vector were significantly correlated across the two skin surfaces ($r(17) = 0.57$, $p < 0.05$), radial components were not ($r(17) = 0.31$, $p = 0.20$). To further investigate the similarities, we performed paired-samples t-tests for distal and radial bias independently, comparing the grand average CE vector on each skin surface. Distal bias was significantly greater on the hairy than the glabrous skin surfaces ($t(18) = 11.58$, $p < .001$, $d = 2.66$), and radial bias was almost significantly greater as well ($t(18) = 2.03$, $p = 0.06$, $d = 0.47$).

We replicated the findings of Mancini and colleagues (2011) on the hairy skin surface of the hand, showing that there are significant distal and radial biases in

localisation error, with radial biases being smaller in magnitude than distal biases. However, we did not find as they did that biases are stronger for points closer to the wrist, but we found that biases were stronger for more distal points and points closer to the thumb. Moreover, on the glabrous skin surface of the hand, we do not find a weak proximal bias and no radial bias like Mancini et al. (2011). While biases are weaker on the glabrous skin than the hairy skin surface of the hand, we found localisations were still significantly biased in distal and radial directions on the glabrous skin. Both distal and radial components of constant error on the glabrous skin increased in magnitude for points closest to the wrist, which also differed from the results reported by Mancini et al., that only the most distal point closest to thumb showed an increase in bias compared to other points.

Tactile localisation on the foot

The left panel of Figure 5.3 shows the average position of actual and judged points on the *hairy* skin of the foot. There was a significant distal component of the grand average CE vector ($t(18) = 11.14$, $p < 0.001$, $d = 2.56$), which was on average biased by 1.61 Bookstein units (± 0.14). Distal components of each CE vector differed significantly across the nine locations on the hairy skin of the foot ($F(8,144) = 62.51$, $p < 0.001$, $\eta_p^2 = 0.78$). Consistent with our findings on the hairy skin of the hand, Bonferroni-corrected post-hoc comparisons showed that distal bias increased from the left to the right side of the foot (towards the big toe), as each column of locations was significantly different from each other (all $p < 0.001$). Distal bias was also greater for points closest to the toes, as this row was significantly different from the middle row and

the bottom row of points (both $p < 0.001$), although the middle and bottom rows were not significantly different from one another ($p = 0.81$).

There was no significant radial component of the grand average CE vector (t(18) = -1.32, p = 0.20, d = -0.30), which was on average biased by -0.02 Bookstein units (± 0.02). Radial components of CE vector did not differ across the nine stimulated locations on the hairy skin of the foot ($F(8,144) = 0.74$, $p = 0.66$, $\eta_p^2 = 0.04$).

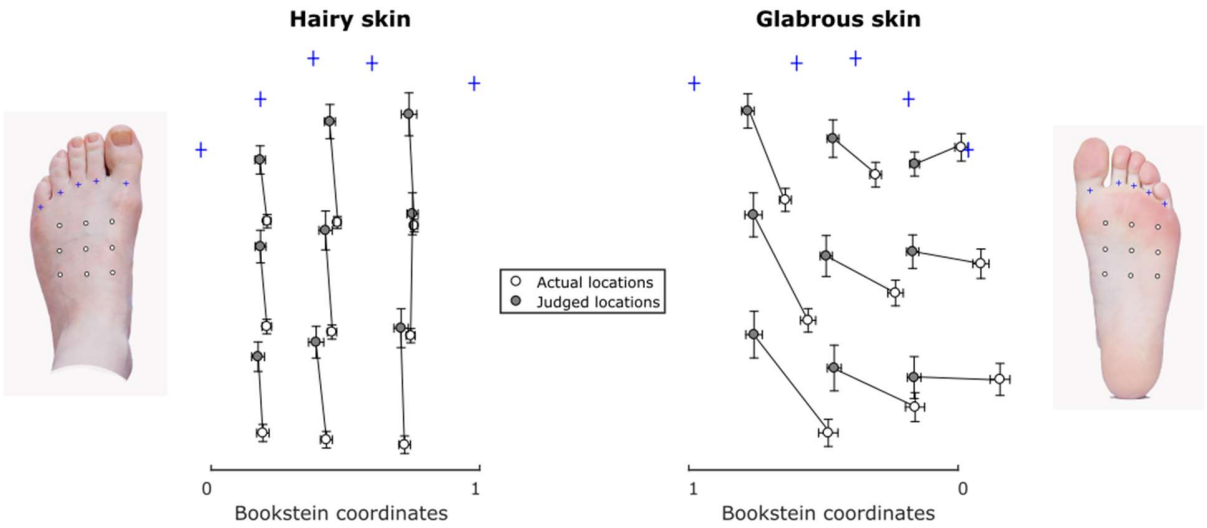

Figure 5.3. Perceptual map of touch on the hairy skin (left) and glabrous skin (right) of the left foot. The average actual (white circles) and judged (grey circles) locations of the nine stimulated points on the foot are plotted in Bookstein coordinates, centred on the outermost edge of the little toe (0,0) and the outermost edge of the big toe (1,0). Although the foot was not turned during testing, the data is presented as though it was, looking *directly at* the stimulated skin surface. As such, the big toe is located to the *right* of all points on the hairy skin, and the *left* of all points on the glabrous skin. Blue crosses indicate the locations of the base of each toe. Error bars represent SE.

The right panel of Figure 5.3 shows the average position of actual and judged points on the *glabrous* skin of the foot. There was a significant distal component of the grand average CE vector ($t(18) = 2.24$, $p < 0.05$, $d = 0.52$), which was on average biased by 0.12 Bookstein units (± 0.06). Distal bias differed significantly across the nine

stimulated locations on the glabrous skin of the foot ($F(8,144) = 23.52$, $p < 0.001$, $\eta_p^2 = 0.57$). Bonferroni-corrected post-hoc comparisons showed that distal bias increased towards the big toe, as each column of locations was significantly different from one another (all $p < 0.001$).

There was also a significant radial component of grand average CE vector ($t(18) = 9.48$, $p < 0.001$, $d = 2.18$), which was on average biased by 0.23 Bookstein units (± 0.02). Radial bias also differed across the nine stimulated locations ($F(8,144) = 11.24$, $p < 0.001$, $\eta_p^2 = 0.38$). Bonferroni-corrected post-hoc comparisons showed that magnitude of bias increased towards the ankle joint and decreased towards the digits (all $p < 0.001$).

Neither distal ($r(17) = 0.19$, $p = 0.44$) nor radial ($r(17) = -0.06$, $p = 0.82$) components of CE were correlated across the two skin surfaces of the foot. As for the hand, we performed paired-samples t-tests for distal and radial bias independently, comparing the grand average CE vector on each skin surface. Distal bias was significantly greater on the hairy than the glabrous skin surface ($t(18) = 10.28$, $p < .001$, $d = 2.36$), as we also found on the hand. However, radial bias was significantly greater on the glabrous than the hairy skin ($t(18) = -8.51$, $p < 0.001$, $d = -1.95$).

Similarities in tactile localisation on the hand and foot

To directly compare performance on the hand and the foot, measures of bias were converted from Bookstein coordinates to cm, as detailed in the *Analysis* section. We performed repeated-measures ANOVAs with two factors: Body Part (hand/foot) and

Skin Surface (hairy/glabrous), with distal and radial components of CE tested separately as dependent variables.

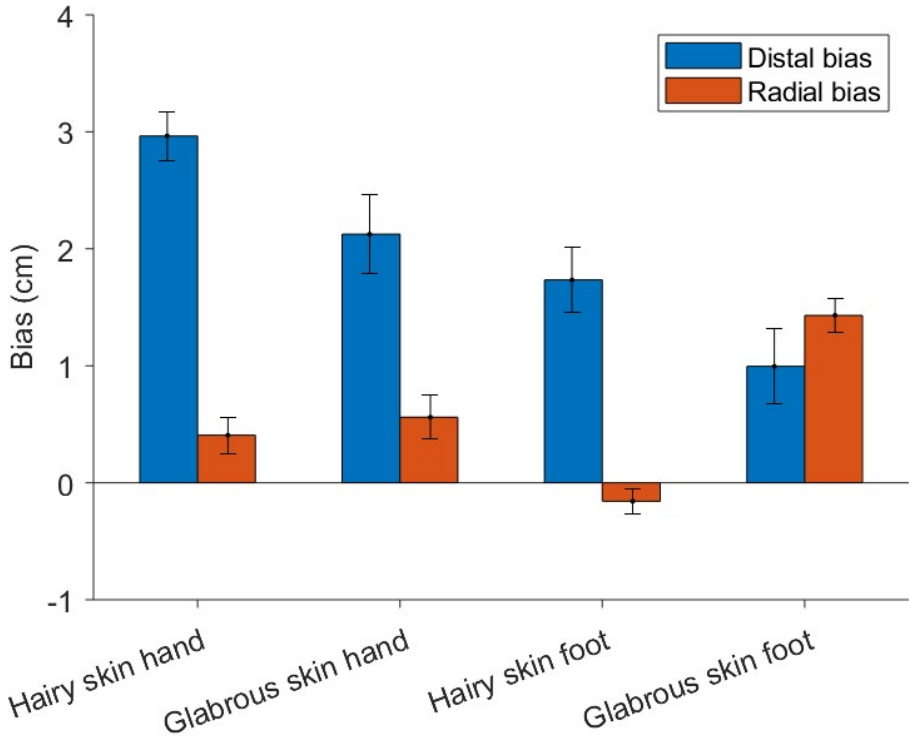

Figure 5.4. Distal bias (left) and radial bias (right) in cm, for each of the four possible stimulated surfaces. Error bars represent standard error of the mean. There were stronger distal biases on the hairy skin of both the hands and the feet, although biases were stronger on the hands than the feet overall. There were stronger radial biases on the glabrous skin of the feet, but not the hands.

The results of the first ANOVA showed that distal bias was significantly greater on the hand than it was on the foot ($F(1,18) = 10.84$, $p = 0.0001$, $\eta_p^2 = 0.38$). Distal bias was also significantly greater on the hairy skin than the glabrous skin surfaces ($F(1,18) = 16.90$, $p < 0.0005$, $\eta_p^2 = 0.48$), as described earlier for both the hand and foot. There

was no significant interaction between body part and skin surface ($F(1,18) = 0.09$, $p = 0.77$, $\eta_p^2 = 0.01$).

The results of the second ANOVA on radial components of CE showed that there was no significant difference between performance on the hand and foot ($F(1,18) = 0.91$, $p = 0.35$, $\eta_p^2 = 0.05$). However, there was a significant effect of skin surface ($F(1,18) = 66.24$, $p < 0.0001$, $\eta_p^2 = 0.79$), and a significant interaction ($F(1,18) = 37.54$, $p < 0.0001$, $\eta_p^2 = 0.68$). Radial bias was greater on the glabrous skin of both the hand and foot, although this difference was only significant between the two skin surfaces of the foot ($t(18) = 8.86$, $p < 0.0001$, $d = 2.10$), and not the hand ($t(18) = 1.14$, $p = 0.27$, $d = 0.27$).

Neither distal ($r(17) = 0.02$, $p = 0.92$) or radial biases ($r(17) = 0.16$, $p = 0.50$) were correlated across the hairy skin surfaces of the hands and feet, nor was radial bias across the glabrous skin surfaces of the hands and feet ($r(17) = -0.21$, $p = 0.40$). Distal bias was correlated across the glabrous skin surface of the hands and feet ($r(17) = 0.49$, $p < 0.05$).

Analysis of variable error

In addition to investigating how CE varied across the two skin surfaces of the hand, we also investigated how variable error (VE; the standard deviation of multiple responses) differed, as shown in Figure 5.5. We performed a repeated-measures ANOVA with two factors: Error Direction (distal/radial) and Skin Surface (hairy/glabrous), and VE as the dependent variable. The results of the ANOVA revealed that VE was greater in the proximo-distal than the medio-lateral direction ($F(1,18) =$

19.22, $p < 0.001$, $\eta_p^2 = 0.52$), as has been reported in previous studies (Margolis & Longo, 2014; Medina et al., 2018; Sadibolova, Tamè, Walsh, et al., 2018). Paired-samples t-tests showed that VE was greater in the proximo-distal than the medio-lateral direction on the hairy skin surface of the hand ($t(18) = 3.22$, $p < 0.01$, $d = 0.74$) and the glabrous skin surface ($t(18) = 2.89$, $p = 0.01$, $d = 0.66$). Moreover, VE was also greater on the hairy skin than the glabrous skin surface ($F(1,18) = 23.35$, $p < 0.001$, $\eta_p^2 = 0.57$). There was no significant interaction ($F(1,18) = 2.07$, $p = 0.17$, $\eta_p^2 = 0.10$).

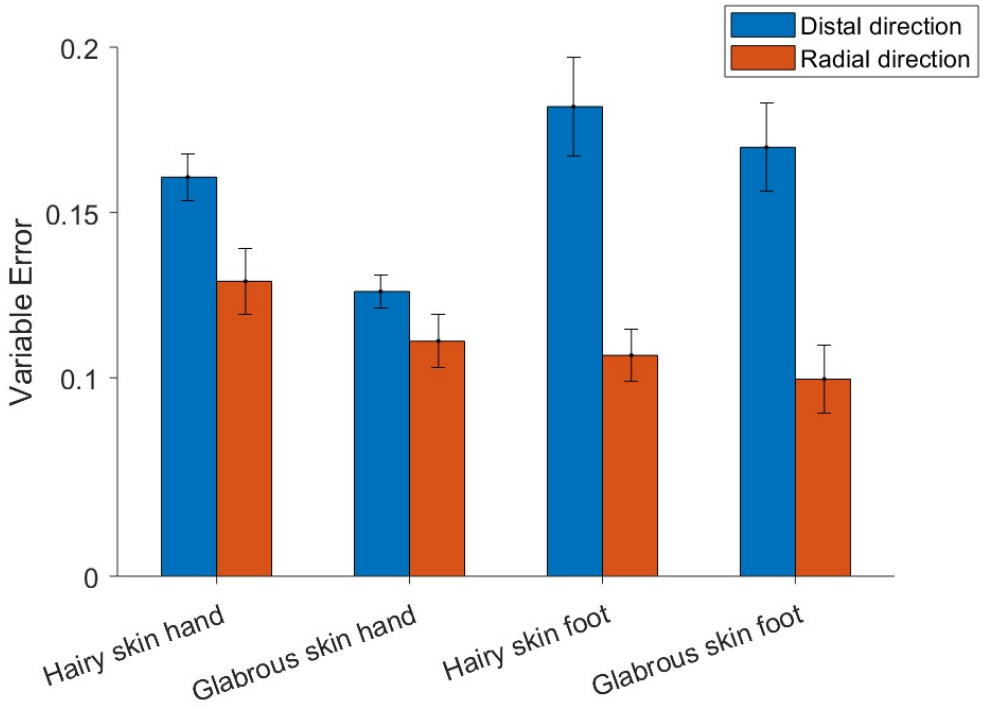

Figure 5.5. Proximo-distal VE (left) and medio-lateral VE (right) for the hairy and glabrous skin of the hand and foot. VE was greater in the proximo-distal than medio-lateral direction on both the hand and foot. VE was also greater on the hairy skin than the glabrous skin of both the hand and foot. Error bars represent SE.

We again investigated how VE differed across the two skin surfaces of the feet by performing a repeated-measures ANOVA with the same factors. The results of the

ANOVA revealed that VE was greater in the proximo-distal than the medio-lateral direction ($F(1,18) = 77.39$, $p < 0.001$, $\eta_p^2 = 0.81$), as was found on the hand. Paired-samples t-tests again showed that VE was greater in the proximo-distal than the medio-lateral direction on the hairy skin surface ($t(18) = 7.07$, $p < 0.001$, $d = 1.62$) and the glabrous skin surface of the foot ($t(18) = 7.61$, $p < 0.001$, $d = 1.75$). However, there was no effect of Skin Surface ($F(1,18) = 2.34$, $p = 0.14$, $\eta_p^2 = 0.12$), or significant interaction between Skin Surface and Error Direction ($F(1,18) = 0.21$, $p = 0.65$, $\eta_p^2 = 0.01$).

We also investigated how variable error differed across the two skin surfaces of the hands and feet. We performed a repeated-measures ANOVA with three factors: Error Direction (distal/radial), Skin Surface (hairy/glabrous), and Body Part (hand/foot). The results of the ANOVA showed that VE was greater in the proximo-distal than the medio-lateral direction ($F(1,18) = 94.71$, $p < 0.001$, $\eta_p^2 = 0.84$), VE was greater on the hairy than the glabrous skin surface ($F(1,18) = 17.36$, $p < 0.001$, $\eta_p^2 = 0.49$), and VE was greater on the feet than on the hands ($F(1,18) = 49.19$, $p < 0.001$, $\eta_p^2 = 0.73$). Moreover, there was a significant interaction between body part and bias direction ($F(1,18) = 39.16$, $p < 0.001$, $\eta_p^2 = 0.69$). Bonferroni-corrected paired-samples t-tests showed that distal components of VE on the foot were stronger than distal components of VE on the hand ($t(18) = 9.30$, $p < .001$, $d = 2.13$), radial components of VE on the foot ($t(18) = 11.33$, $p < .001$, $d = 2.60$), as well as radial components of variable error on the hand ($t(18) = 11.23$, $p < .001$, $d = 2.58$). None of the remaining comparisons were significant (all $p > 0.05$).

5.4. Discussion

In this study we investigated tactile localisation on the hairy and glabrous skin surfaces of the hands and feet. We replicated the findings of Mancini et al. (2011), finding consistent biases in localisation on the hairy skin surface of the hand in a distal and radial direction, which increase in magnitude for points towards the knuckles and thumb. We found that localisation biases on the glabrous skin surface of the hand were consistent with this pattern, although biases increase in magnitude for points towards the wrist, in contrast to the small proximal bias found by Mancini and colleagues. On the hairy skin surface of the foot, we found strong distal biases in localisation that increased for points close to the big toe, comparable to the pattern found on the hairy skin of the hand. On the glabrous skin surface of the foot we found a smaller but consistent distal bias, which also increased for points close to the big toe. We also found radial biases in mislocalisation that increased in magnitude for point close to the ankle, consistent with the finding on the glabrous skin surface of the hand that biases increased for points close to the wrist.

The results of this experiment support the theory proposed by Mancini et al. (2011) that differences in the magnitude of localisation biases across the hairy and glabrous skin surfaces of the hand may arise from the smaller and less elongated RFs on the glabrous skin of the hand compared to the hairy skin (DiCarlo & Johnson, 2002; DiCarlo et al., 1998). Like Mancini and colleagues found on the glabrous skin surface of the hand, magnitude of localisation biases in our study were reduced on the glabrous skin surface of the foot compared to the hairy skin surface. RFs for the hairy skin surface of the hands and feet appear to be similar in size and shape (Vedel & Roll,

1982), but RFs for the glabrous skin surface of the foot appear to be bigger than those for the hand (Strzalkowski et al., 2018). We are not aware of any studies that directly compare RF properties of the two skin surfaces of the feet, however, that we find smaller biases on the glabrous skin of the foot than the hairy skin suggests that RFs of the glabrous skin remain smaller than those found on the hairy skin surface (like the hand).

Like Mancini and colleagues, we found consistent distal and radial biases in localisation on the hairy skin surface on the hand. On the glabrous skin surface of the hand, in contrast to the small proximal bias found by Mancini et al., we found consistent distal and radial biases in localisation. Our results (but not those of Mancini and colleagues) are consistent with a hypothesis proposed in previous studies, that there is a common representation of the two skin surfaces of the hand in high-level representations of the body (Longo, 2014; Manser-Smith et al., 2018), resulting in quantitively similar patterns of mislocalisations found across the two skin surfaces.

Moreover, in the present study we show that distal biases found on both skin surfaces of the hand are comparable to those found on the hairy skin surface of the foot, as well as the glabrous skin surface of the foot. Radial biases were less consistent across all skin surfaces tested – there is a weaker radial bias on the hairy skin surface of the foot than the hand, but there is a stronger radial bias on the glabrous skin surface of the foot than on the hand. However, on both the hand and foot, magnitude of radial biases increased towards the wrist or ankle joint, respectively. These results are consistent with a hypothesis proposed in a previous study (Manser-Smith et al., 2019) – quantitatively

similar patterns of mislocalisation bias across the hands and feet may arise from a common higher-order representation of the hands and feet.

As well as analysing constant error in this study we also investigated variable error, the standard deviation of multiple responses, and a measure of the imprecision of localisation. As in previous studies (Margolis & Longo, 2014; Medina et al., 2018; Sadibolova, Tamè, Walsh, et al., 2018), variable error was greater along the proximo-distal axis than the medio-lateral axis on the hairy skin surface of the hand. On the glabrous skin surface of the hand magnitude of variable error was significantly decreased, although still greater along the proximo-distal than the medio-lateral axis of the hand. These findings are also replicated on the foot – localisation was more accurate in the medio-lateral axis than the proximo-distal axis, with magnitude of bias reduced on the glabrous skin compared to the hairy skin. Interestingly, magnitude of variable error along the proximo-distal axis was greater on the hairy skin surface of the foot than on the hairy skin surface of the hand, whereas magnitude of constant error along this axis was greater on the hand than on the foot. These findings support the conclusions made by previous studies that differences in variable error also arise from differences in RF size and shape across these skin surfaces (Mancini et al., 2011; Margolis & Longo, 2014; Sadibolova, Tamè, Walsh, et al., 2018).

One concern in the present study is the magnitude of localisation biases found on the two skin surfaces of the hand. As can be seen in Figure 5.2, participants responses suggest that they perceived the touches on the hand as much more distally than their actual location, in some cases above the knuckles and onto the fingers. Although the direction of our biases follows the same pattern as Mancini et al. (2011), the magnitude

of biases they found was almost half of ours – on the hairy skin surface of the hand they found biases of 0.28 Bookstein units, compared to 0.53 in our experiment. Although we kept our methodology as close to that used by Mancini and colleagues as possible, the improbably large biases we have found suggests that there may have been an issue with our calculation of the Bookstein units. However, after reviewing our analysis several times we could not identify where this issue may have arisen. We believe that it is likely to have arisen from the calculation of Bookstein units as the direction of biases found are overall similar to those found by Mancini et al. (2011), though increased in magnitude, suggesting a multiplication error at some point in our analyses.

Overall, the results of the present study support the assertions of Mancini and colleagues (2011), that differences in RF size and shape across the hairy and glabrous skin surfaces of the hand result in greater magnitude of localisation biases on the hairy skin than the glabrous skin surfaces of the hand. We further show that this is also true across the two skin surfaces of the feet, and that biases in variable error also conform to this pattern of results. In contrast to Mancini and colleagues, we found that direction of biases were highly consistent across the hairy and glabrous skin surfaces of both the hands and feet, providing further evidence that there are common high-level representations of the two skin surfaces of hands (Manser-Smith et al., 2018), as well as of the hands and feet (Manser-Smith et al., 2019).

Chapter 6: Distortions of tactile size perception on the hands and feet

6.1. Introduction

Illusions of tactile size perception have been described since the early 19th century, when Weber showed that two points of touch on the skin are perceived as farther apart on highly sensitive skin surfaces, compared to less sensitive regions (Weber, 1834/1996). This effect, known as Weber's illusion, has been found over a range of different body parts, and is systematically related to tactile sensitivity and cortical magnification (i.e., the proportion of cortical area given to a specific skin surface; Cholewiak, 1999; Green, 1982). As well as tactile size perception differing across skin surfaces, the distance between two points is also perceived differently depending on the orientation of the two points on a single skin surface (Green, 1982; Longo & Haggard, 2011). On most body parts studied, tactile distances are perceived as farther apart when going across (medio-lateral axis) the body part, as opposed to along (proximo-distal axis). This anisotropy is consistent across a number of body parts, including the hand (Green, 1982; Longo & Haggard, 2011), forearm (Fiori & Longo, 2018), forehead (Longo, Ghosh, et al., 2015), and the leg (Stone et al., 2018). Nevertheless, the magnitude of such anisotropies varies across the body, suggesting that there are important differences in the representation of the skin of different body parts.

These anisotropies in tactile size perception are thought to arise from corresponding anisotropies in receptive field (RF) size on the hairy skin surface (Green, 1982; Longo & Haggard, 2011). According to the pixel model, proposed by Longo and Haggard (2011) tactile space consists of a 2D array in which individual RFs form the

pixels. Perceived size is measured by the number of RFs between two stimulated locations. On the hairy skin, RFs are generally oval-shaped, with the long axis running proximodistally (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961; Brown, Fuchs, & Tapper, 1975; as cited in Longo & Haggard, 2011). As such, perceived size is greater when two stimulated locations are oriented across the body part than along, as there are a greater number of receptive fields between two points along the medio-lateral axis than the proximo-distal axis. On the hairy skin surface of the hand, for example, objects touching the skin are perceived as 40% larger when they are oriented across the hand than along it (Longo & Haggard, 2011). On the glabrous skin, however, RFs are generally smaller and less elongated than on the hairy skin (DiCarlo & Johnson, 2002; DiCarlo et al., 1998). As such, anisotropies in tactile size perception on the glabrous skin of the hand are reduced (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015), or non-existent (Longo & Golubova, 2017; Longo & Haggard, 2011) relative to those on the hairy skin surface of the hand.

To our knowledge, whether anisotropies such as those reported on the hairy skin surface of the hand, or other body parts, are present on either skin surface of the feet has not been tested. Previous studies have shown that there are anisotropies in tactile size perception on the thigh (Green, 1982) and shin (Stone et al., 2018), suggesting that anisotropies may be a shared characteristic between the arms and legs. Whether there are anisotropies in tactile size perception on the feet is an intriguing question given the similarities and differences between the hands and the feet. The hands and the feet are serially homologous (Rolian et al., 2010), meaning they share a qualitatively similar structural plan (Owen, 1849/2008), five digits on each body part, and the presence of

both a hairy and glabrous skin on their alternate sides (Marieb, 2012). Beyond their physical similarities, there are also deeper levels of similarity in how the hands and feet are represented in the somatosensory cortex, and higher cortical areas related to body representation. Both the fingers and toes are represented separately from the rest of the hand and foot in S1 of non-human primates (Merzenich et al., 1978; Nelson et al., 1980), and there is evidence to suggest that this distinction is conserved in humans. For example, individuals with finger agnosia experience the selective loss of ability to recognise, identify, distinguish or indicate individual fingers, on either the patient's own or another's fingers (Anema et al., 2008; Gerstmann, 1939; Kinsbourne & Warrington, 1962; Mayer et al., 1999). In healthy participants, a behavioural study using predictive cuing of stimuli applied to the palm or fingers of the hand has shown that cuing facilitates or hinders localisation on the two body parts differently (Gálvez-García et al., 2012). Moreover, 7T neuroimaging has shown that the thumb (Martuzzi et al., 2014) and big toe (Akselrod et al., 2017), at least, are represented separately from the rest of the hand and foot, respectively.

Despite these similarities, there are a number of obvious differences between the hand and the foot: despite having the same underlying bone structure, the hand and the foot are very different in their size and shape (Marieb, 2012), as well as having widely different uses in humans. Some less obvious differences are that there are fewer slow-adapting mechanoreceptors in the glabrous skin of the foot than the hand, and these mechanoreceptors, as well as fast-adapting type 1 receptors, have much higher activation thresholds in the glabrous skin of the foot (Kennedy & Inglis, 2002). Differences in tactile sensitivity across the hands and feet make us less accurate at

localising touch to individual toes than to individual fingers (Cicmil et al., 2016). When tactile confusions do occur between the digits, the pattern of incorrect identifications (i.e. mislocalisations) is different on the fingers and toes – the fingers are biased towards the middle finger of the hand, and the toes towards the big toe for the fourth toe, and the little toe for the second and third toes (Braun et al., 2011; Braun, Ladda, et al., 2005; Cicmil et al., 2016; Halnan & Wright, 1960; Manser-Smith et al., 2018; Schweizer et al., 2001).

The aim of this study is to investigate whether there are anisotropies in tactile distance perception on the two skin surfaces of the foot, such as there are on the hand, and whether they are similar or different on the hairy and glabrous skin. We will do this using testing and analysis methods very similar to previous studies testing the hand (Longo, Ghosh, et al., 2015; Longo & Haggard, 2011). The presence of anisotropies on the feet similar to those found on the hand would suggest that anisotropies may be a general characteristic of the representations of the limbs. All procedures, including sample size, exclusion criteria, and analysis plans were pre-registered on the Open Science Framework (osf.io/npkhc).

6.2. Experiment 1

6.2.1. Methods

Participants

A number of studies have been conducted investigating anisotropies in tactile size perception on the hairy skin of the hand. To conduct a power analysis to find the appropriate number of participants for the present study, we took effect sizes from 19

studies conducted by Longo and colleagues (total N = 394), resulting in a weighted average Cohen's *d* of 1.50. We conducted a power analysis using G*Power (Faul et al., 2007) with this effect size, an alpha value of 0.05 and power of 0.95, which indicated 7 participants would be required for sufficient power. While anisotropy on the foot may be smaller than on the hand, we expect a broadly comparable magnitude of anisotropy.

We recruited 20 participants, though one participant was removed from analyses (see Analysis section). As such, 19 participant's data were analysed (10 female; mean age = 27 years; range = 20 - 46). This gave us a power of over 90% to detect an effect of even half the size as that found on the hand. Participants all reported normal or corrected-to-normal vision and normal touch. All 19 participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean = 69.24, range = 37.50 – 95.80). Of the 19 right-handed participants, 18 were right-foot dominant and one participant was left-foot dominant, as assessed by the Waterloo Footedness Questionnaire (Elias, Bryden, & Bulman-Fleming, 1998; mean = 52.10, range = -5.00 – 100). EHI and WFQ scores were strongly correlated across participants ($r = 0.74$, $p < 0.0001$). All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

Stimuli

Tactile stimuli were pairs of wooden posts mounted in foamboard, separated by 20, 30, or 40mm, as in previous studies (Longo, Ghosh, et al., 2015; Longo & Haggard, 2011). The ends of the wooden posts were tapered to a point, but not sharp.

Figure 6.1. Experimental set-up for Experiments 1, 2 and 3. During Experiments 1 and 3, participants sat with their left foot rest on a stool, and arms resting on the arm rests of the chair. During Experiment 2, participants sat with their left foot resting on a stool and left hand resting on a table (as shown above). Participants were blindfolded in all experiments.

Task

The procedures closely followed those used in several previous studies from our lab (Longo, 2017; Longo, Ghosh, et al., 2015; Longo & Haggard, 2011; Longo & Morcom, 2016). Participants were evaluated on their hand and foot dominance, though all participants were tested on their left foot, regardless of assessed foot dominance. Participants were seated in a comfortable position with their left foot resting on a stool (Fig. 6.1), and were asked to remain as still as possible throughout each experimental block. On each trial, participants were touched twice on the hairy skin or glabrous skin of the left foot, once with the posts oriented along the proximodistal axis of the hand (along stimulus), and once oriented along the mediolateral axis (across stimulus). Touch

was applied manually, approximately in the center of either surface of the foot, and with moderate pressure. The duration of each touch was approximately one second, with an interstimulus interval of approximately one second. Participants made untimed two-alternative forced choice judgments of whether the first or second stimulus felt larger (i.e. the two points felt farther apart) and responded verbally. Participants were blindfolded throughout the procedure but were briefly shown the 30mm stimuli only before testing commenced to familiarise themselves with the stimuli.

There were four blocks, two in which the hairy skin surface of the foot was tested, and two in which the glabrous skin surface of the foot were tested. ABBA counterbalancing was used to vary order of presentation, with the first condition counterbalanced across participants. Each block contained 100 trials, resulting in 20 trials per block for each of the five stimulus pairings (across/along): 20/40 mm, 20/30 mm, 30/30 mm, 30/20 mm, and 40/20 mm. Therefore, there was a total of 400 trials, and 80 trials per stimulus pairing. The order of along and across stimuli was counterbalanced within each stimulus pair, and the order of the trials was randomised and shown to the experimenter through a custom MATLAB script.

Analysis

The proportion of trials in which the 'across' stimulus was judged as larger was analysed as a function of the ratio of the length of the along and across stimuli. The ratios of the five stimulus pairings (described above) expressed as numerical values are 0.5, 0.67, 1, 1.5 and 2. As these values are not symmetrically distributed around the point-of-actual-equality (i.e. where the ratio equals 1), they were logarithmically

transformed to produce a symmetrical distribution. Calculation of means and all statistical tests were conducted on the log-transformed values, which were converted back to ratios for reporting for ease of understanding. Cumulative Gaussian functions were fitted to each participant's data on each skin surface, using maximum-likelihood estimation with the Palamedes toolbox for MATLAB (Prins & Kingdom, 2009). For each curve, we obtained: (1) the *point of subjective equality* (PSE; i.e., the mean of the Gaussian), that is the point at which the psychometric function crosses 50%; (2) the *slope* of the psychometric function (i.e., the inverse of the standard deviation of the Gaussian); and (3) the R^2 value, the proportion of the variance in the mean values across the 5 trial types accounted for by the psychometric function. Participants with an R^2 value less than 0.5 for either the hairy or glabrous skin surface were excluded from the analysis, as this indicates poor fit of the data (Longo, Ghosh, et al., 2015; Longo & Morcom, 2016). One participant had R^2 values below 0.5 on both the hairy and glabrous skin surfaces, and was therefore excluded from the analysis. Of the remaining participants, R^2 values ranged from 0.67 to 1 (M = 0.94, SD = 0.08) on the hairy skin and 0.83 to 1 (M = 0.96, SD = 0.04) on the glabrous skin, indicating good fit of the data.

Initially, we investigated whether there are anisotropies in tactile distance perception on the foot. We conducted two one-sample t-tests comparing the PSEs on the hairy skin and glabrous skin of the foot to 1 (i.e. no bias in responding). We also investigated similarity of tactile distance perception across the hairy and glabrous skin of the foot, first by correlating PSE values for each participant across the two skin surfaces. We also carried out a paired-samples t-test between PSE values on the hairy and glabrous skin surfaces.

6.2.2. Results and discussion

Figure 6.2 shows the grand average results with best-fitting psychometric functions, on the hairy and glabrous skin surfaces of the foot. A PSE equal to 1 would indicate that stimulus orientation did not affect perceived size. If PSE is greater than 1, this would indicate a bias to judge stimuli aligned with the length of the foot as larger than stimuli aligned with the width of the foot. A PSE smaller than 1, in contrast, would indicate a bias to judge stimuli aligned with the width of the foot as larger than stimuli aligned with the length of the foot.

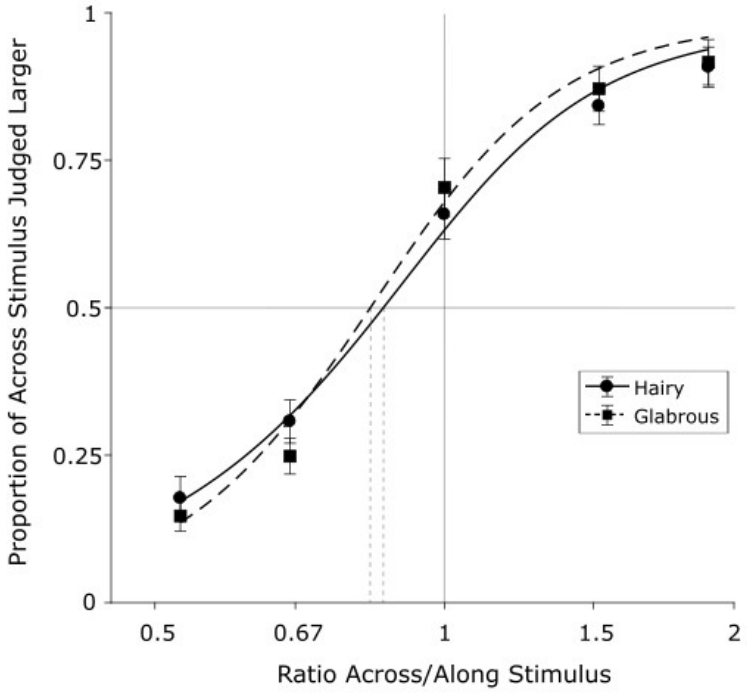

Figure 6.2. Results from Experiment 1. The curves are cumulative Gaussian functions fit with maximum-likelihood estimation. Error bars represent the standard error of the mean. The solid vertical line crossing 1 on the x-axis represents the point of subjective equality if there was no anisotropy (i.e., where 50% of stimuli are judged as larger). The dashed vertical lines represent the grand average PSE for both the hairy and glabrous skin surfaces. The x-axis is plotted with log-transformed stimulus ratios to create an equal distribution around the point of subjective equality. However, the value labels are actual ratios values, for ease of understanding as this is consistent with the reporting in text.

All analyses were carried out on log transformed values and transformed back into ratios for reporting. The mean PSE for the hairy skin of the foot was 0.83, significantly less than 1, $t(18) = -6.50$, $p < 0.001$, $d = -1.49$, indicating a bias to represent the foot as wider than it really is. Out of 19 participants, 18 showed this bias, in that PSEs for every participant except one were less than 1 (range = 0.64 – 1.01). This finding is very similar to previous results from the hairy skin of the hand (Longo, Ghosh, et al., 2015; Longo & Haggard, 2011).

The mean PSE for the glabrous skin of the foot was 0.82, significantly less than 1, $t(18) = -4.43$, $p < 0.001$, $d = -1.02$. Out of 19 participants, 16 showed this bias (range = 0.56 – 1.07). These results are strikingly similar to those found on the hairy skin of the foot, although they differ from previous results on the glabrous skin of the hand, where non-existent (Longo & Golubova, 2017; Longo & Haggard, 2011) or smaller (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015) anisotropies were found compared to the hairy skin surface of the hand .

PSEs on the hairy and glabrous skin surfaces of the foot were strongly correlated, $r(18) = 0.73$, $p < 0.001$. A paired-samples t-test confirmed that there was no significant difference between the PSE scores on the hairy and glabrous skin surfaces, $t(18) = 0.10$, $p = 0.93$, $d = 0.02$.

These results show that biases in tactile distance perception are also evident on the hairy skin surface of the foot – like the hairy skin surface of the hand, the foot was perceived as wider than it is. Intriguingly, we also found anisotropies in tactile distance perception on the glabrous skin surface of the foot of the same magnitude as on the hairy skin of the foot. These findings suggest that anisotropies in tactile distance perception

are a general characteristic of the limbs, as we find similar results on the hairy skin of the hands and both skin surfaces of the feet. That anisotropies in tactile distance perception are reduced or non-existent on the palm of the hands indicates that this skin surface is in some way special – the glabrous skin surface of the hand is important for goal directed actions, such as skilled instrumental action and haptic object manipulation. As such, anisotropies may be reduced on the glabrous skin of the hand in order to carry out these actions with higher precision.

6.3. Experiment 2

The aim of this study is to replicate the anisotropies in tactile distance perception found on both skin surfaces of the feet in Experiment 1, and directly compare tactile distance perception on the hairy and glabrous skin of both the hands and feet in the same participants. We did this using testing and analysis methods very similar to Experiment 1.

6.3.1. Methods

Participants

The results of Experiment 1 showed Cohen's *d* values of 1.49 and 1.01 on the hairy and glabrous skin surfaces of the foot, respectively. We conducted a power analysis using G*Power (Faul et al., 2007) with the smallest effect size from Experiment 1, an alpha value of 0.05 and power of 0.95, which indicated 13 participants would be required for sufficient power. We aimed to recruit 20 participants, as participants completed fewer trials per skin surface than in our previous experiment.

We recruited 20 participants (12 female; mean age = 27 years; range = 18 - 46). This gave us a power of over 90% to detect an effect of even half the size as that found on the hand. Participants all reported normal or corrected-to-normal vision and normal touch. Of the 20 participants tested, 19 were right-handed and one left-handed (mean = 62.5, range = -90 – 100). The same 19 participants were right-foot dominant, and one left-foot dominant (mean = 52.8, range = -75 – 100). EHI and WFQ scores were strongly correlated across participants ($r = 0.67$, $p < 0.001$). All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

Task

The procedures closely followed those used in Experiment 1. All participants were tested on their left hand and foot, regardless of assessed hand and foot dominance. Participants were seated in a comfortable position with their left foot resting on a stool, and their left hand resting on a table (Fig. 6.1). On each trial, participants were touched twice on the hairy skin or glabrous skin of the left hand or foot, once with the posts oriented along the proximodistal axis of the hand/foot (along stimulus), and once oriented along the mediolateral axis (across stimulus). Touch was applied manually, approximately in the centre of either surface of the hand or foot, and with moderate pressure. Stimuli used were the same as in Experiment 1.

There were eight blocks, two in which the hairy skin surface of the hand was tested, two on the glabrous skin surface of the hand, two on the hairy skin surface of the foot, and two on the glabrous skin surface of the foot. Latin-square counterbalancing

was used to vary order of presentation for the first four blocks, and this order reversed for the next four blocks. Each block contained 50 trials, resulting in 10 trials per block for each of the five stimulus pairings (across/along): 20/40 mm, 20/30 mm, 30/30 mm, 30/20 mm, and 40/20 mm. Therefore, there was a total of 400 trials, and 20 trials per stimulus pairing on each skin surface. The order of along and across stimuli was counterbalanced within each stimulus pair, and the order of the trials was randomised and shown the experimenter through a custom MATLAB script.

Analysis

Analyses closely followed Experiment 1. R^2 values for all participants in Experiment 2 were above 0.5, on the hairy ($M \pm SD$, range; 0.94 ± 0.07, 0.72 - 0.99) and glabrous skin surfaces of the foot (0.93 ± 0.08, 0.67 - 0.99), and the hairy (0.95 ± 0.05, 0.79 - 0.99) and glabrous skin surfaces of the hand (0.97 ± 0.07, 0.69 - 1).

For each of the two body parts, we investigated whether there are anisotropies in tactile distance perception on both the hairy and glabrous skin. First, we conducted four one-sample t-tests comparing the PSEs on the hairy skin and glabrous skin of the hand and foot to 1 (i.e. no bias in responding). We investigated similarity of tactile distance perception across the hairy and glabrous skin of the hand and foot, first by correlating PSE values across the two skin surfaces of each body part independently, then by correlating PSE values across the hand and foot, for each skin surface separately. We also compared similarity of tactile distance perception across the hairy and glabrous skin of the hand and foot by running four paired-samples t-tests, firstly comparing PSE values across the two skin surfaces of each body part independently, then comparing

PSE values across the hand and foot, for each skin surface separately. Finally, to compare PSE across both body parts and skin surfaces, we conducted a repeated-measures ANOVA with two factors: SKIN SURFACE (hairy/glabrous) and BODY PART (hand/foot), with PSE as the dependent variable.

6.3.2. Results and Discussion

Figure 6.3 shows the grand average results with best-fitting psychometric function, across the hairy and glabrous skin surfaces of the foot (left panel) and the hand (right panel). The mean PSE for the hairy skin of the foot was 0.84, significantly less than 1, $t(19) = -3.23$, $p < 0.01$, $d = -0.72$, indicating a bias to represent the foot as wider than it really is. Out of 20 participants, 14 showed this bias, in that PSEs for every participant except six were less than 1 (range = 0.55 – 1.26). This finding is very similar to previous results from the hairy skin of the hand, and our findings in Experiment 1.

The mean PSE for the glabrous skin of the foot was 1.12, significantly greater than 1, $t(19) = 2.18$, $p < 0.05$, $d = 0.49$, indicating a bias towards perceiving the foot as longer than it really is. Out of 20 participants, 15 showed this bias, in that PSEs for every participant except 5 were greater than 1 (range = 0.79 – 2.69). These results contradict those of Experiment 1, indicating that although biases in tactile distance perception are consistent across the hairy skin of the foot to the hand, they are not consistent on the glabrous skin of the foot.

PSEs on the hairy and glabrous skin surfaces of the foot were not correlated, $r(19) = -0.16$, $p = 0.51$, and a paired-samples t-test confirmed that there was a significant

difference between the PSE scores on the hairy and glabrous skin surfaces, $t(19) = -3.56$, $p < 0.01$, $d = -0.80$.

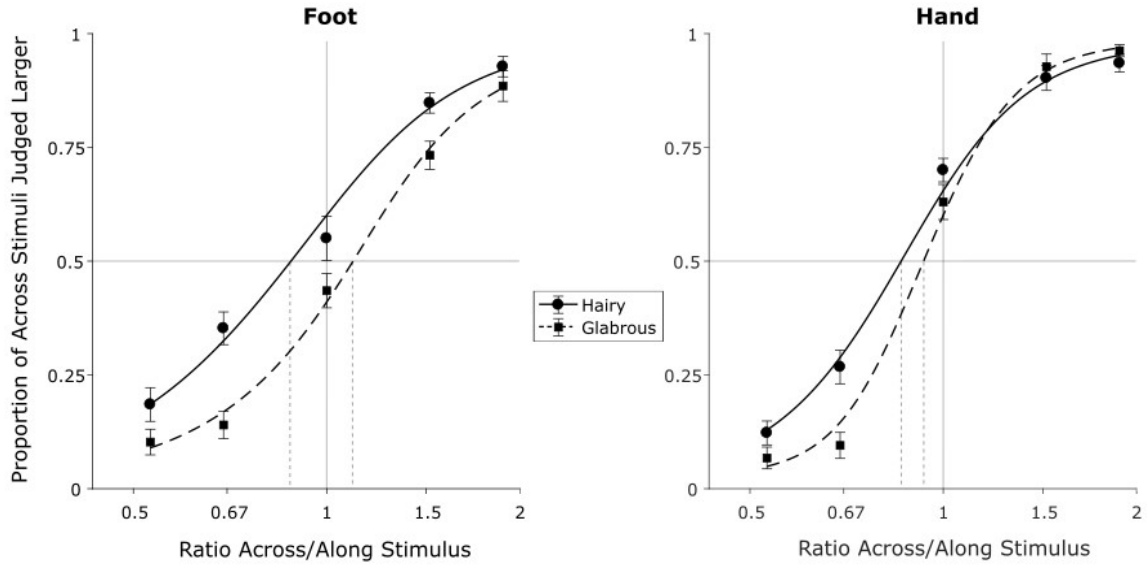

Figure 6.3. Results from Experiment 2. The curves are cumulative Gaussian functions fit with maximum-likelihood estimation. Error bars represent the standard error of the mean. The solid vertical line crossing 1 on the x-axis represents the point of subjective equality if there was no anisotropy (i.e., where 50% of stimuli are judged as larger). The dashed vertical line represents the grand average PSE for both the hairy and glabrous skin surfaces. The x-axis is plotted with log-transformed stimulus ratios to create an equal distribution around the point of subjective equality. However, the value labels are actual ratios values, for ease of understanding as this is consistent with the reporting in text.

The right panel of Figure 6.3 shows the results from experiment 2 on both skin surfaces of the hand. The mean PSE for the hairy skin of the hand was 0.85, significantly less than 1, $t(19) = -6.30$, $p < 0.001$, $d = -1.41$, indicating a bias to represent the hand as wider than it really is. Out of 20 participants, 18 showed this bias, in that PSEs for every participant except two were less than 1 (range = 0.58 – 1.04).

The mean PSE for the glabrous skin of the hand was 0.92, significantly less than 1, $t(19) = -3.18$, $p < .01$, $d = -0.71$. Out of 20 participants, 16 showed this bias (range = 0.64 – 1.18). These results follow previous findings on both skin surfaces of the hand – both skin surfaces are perceived as wider than the hand truly is, although this is reduced on the glabrous skin of the hand.

PSEs on the hairy and glabrous skin surfaces of the hand were again not correlated, $r(19) = -0.10$, $p = 0.67$. A paired-samples t-test confirmed that there was a significant difference between the PSE scores on the hairy and glabrous skin surfaces, $t(19) = -2.05$, $p = 0.05$, $d = -0.46$.

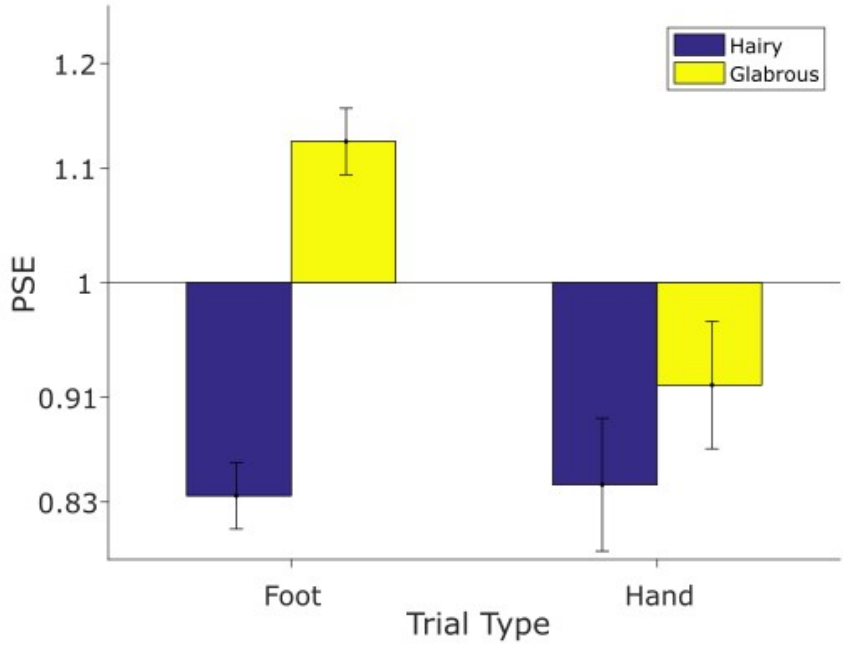

Figure 6.4. Results of Experiment 2 on both hairy and glabrous skin surfaces of the hand and foot. The dashed horizontal axis represents the point of subjective equality if there was no anisotropy (i.e., where 50% of stimuli are judged as larger).

Figure 6.4 shows the grand average PSEs across the hairy and glabrous skin surfaces of the hand and foot. The repeated-measures ANOVA found significant main effects of SKIN SURFACE ($F(1,19) = 29.47$, $p < 0.001$, $\eta^2_p = 0.61$) and BODY PART ($F(1,19) = 6.52$, $p < 0.05$, $\eta^2_p = 0.26$), and a close to significant interaction ($p = 0.07$). PSEs were significantly higher on the glabrous than the hairy skin, and significantly higher on the foot than the hand, both of which were driven by the PSE of the glabrous skin of the foot being greater than 1, indicating a bias to perceive the foot as longer than it is (when all other skin surfaces and body parts were perceived as wider). PSE values were not correlated between the hairy skin surfaces of the hands and feet, $r(19) = -0.02$, $p = 0.93$, and a paired-samples t-test confirmed that there was no significant difference between the body parts, $t(19) = 0.17$, $p = 0.86$, $d = 0.04$, showing that anisotropies in tactile size perception are consistent across the hairy skin surfaces. PSE values were correlated between the glabrous skin surfaces of the hands and feet, $r(19) = -0.50$, $p < 0.05$, although a paired-samples t-test showed that they were significantly different, $t(19) = -2.85$, $p < 0.05$, $d = -0.64$, as the hand was perceived as wider than it is, but the foot was perceived as longer it is.

Experiment 2 again showed that tactile distances were perceived as father apart when going across the hairy skin surface of the hand, as opposed to along. On the glabrous skin surface of the hand we found the same pattern of anisotropies but significantly reduced in magnitude, consistent with previous studies (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015). On the hairy skin surface of the foot, we replicated our findings in Experiment 1 that this skin surface was also perceived as wider than it is. However, on the glabrous skin surface of the foot we found contradictory results to

Experiment 1 – tactile distances were perceived as father apart when going along the foot than across. Thus, Experiments 1 and 2 reached exactly opposite conclusions about the presence of anisotropy on the sole of the foot.

One possible explanation of these contradictory findings on the glabrous skin of the foot in our two experiments is that there were carryover effects between the different skin surfaces we tested. In both our previous experiments all skin surfaces were tested in the same participants, and different skin surface blocks were interleaved – in Experiment 2 the foot blocks were interleaved with blocks of stimulation on the hand, whereas in Experiment 1 only the feet were tested. In Experiment 1, there may have been carryover effects between the two skin surfaces of the foot, resulting in anisotropies of similar magnitude on both the hairy and glabrous skin surfaces, in contrast to the reduced magnitude of anisotropies found on the glabrous skin surface of the hand in previous studies. In Experiment 2, anisotropies on the glabrous skin surface of the foot went in the exact opposite direction of all those previously found, so may not be explained by carryover effects. Instead, we propose that interleaving eight blocks testing four separate skin surfaces within one hour-long experiment may have been cognitively strenuous for participants, causing confusion in their responses. However, it is unclear why this confusion may have disproportionately affected responses made to stimulation applied to the glabrous skin surface of the foot. One possible reason is that the glabrous skin surface of the foot was the only skin surface that was not facing towards the participant. For the hands, participants rotated the hand so either the hairy or glabrous surface was facing up for testing. When either skin surface of the foot was tested, participants remained in the same position with the toes pointing upwards, so that

both skin surfaces could be reached by the experimenter. As such, the glabrous skin surface of the foot was the only skin surface that appeared to be facing away from the participant, potentially differentiating it from the other skin surfaces in participants' responses.

6.4. Experiment 3

The aim of the present experiment is to investigate whether there are anisotropies on both the hairy and glabrous skins surfaces of the foot, independent of any potential carryover effects or confusion in responses. We did this using testing and analysis methods very similar to our previous study, but with independent groups of participants tested on the hairy and glabrous skin surfaces. Because each participant was only tested on one skin surface, the possibility of carry-over effects between skin surfaces is removed.

6.4.1. Methods

Participants

The results of Experiment 1 showed Cohen's *d* values of 1.49 and 1.02 on the hairy and glabrous skin of the foot, respectively. Results from Experiment 1, but not Experiment 2, are used in the power analysis as the number of trials in Experiment 3 will be consistent with Experiment 1 (Experiment 2 had a reduced number of trials). We conducted a power analysis using G*Power (Faul et al., 2007) with the smallest of the effect sizes from our first experiment, an alpha value of 0.05 and power of 0.95, which indicated 13 participants would be required for sufficient power. We aimed to recruit 20

participants per group (testing either the hairy or glabrous skin surface), resulting in a total of 40 participants.

We recruited 40 participants, though one participant was removed from the analyses (see Analysis section). As such, 20 participant's data were analysed for the hairy skin surface of the foot (14 female; mean age = 29.65, range = 18 – 58), and 19 for the glabrous skin surface (12 female; mean age = 27.79, range = 20 – 47). Participants all reported normal or corrected-to-normal vision and normal touch. Of the 20 participants tested on the hairy skin surface of the foot, 19 were right-handed, and one left-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean = 67.50, range = -50.00 – 95.00). The 19 right-handed participants were also right-foot dominant, and the left-handed participant was left-foot dominant, as assessed by the Waterloo Footedness Questionnaire (Elias, Bryden, & Bulman-Fleming, 1998; mean = 35.00, range = -95.00 – 95). EHI and WFQ scores were strongly correlated across participants ($r = 0.84$, $p < 0.001$). All of the 19 participants tested on the glabrous skin surface of the foot were right-handed (mean = 69.74, range = 20 – 100) and right-foot dominant (mean = 57.11, range = 5 – 100), and scores were correlated ($r = 0.52$, $p < 0.05$). All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

Task

The procedures closely followed those used in Experiment 1 and Experiment 2. Participants were evaluated on their hand and foot dominance, though all participants

were tested on their left foot, regardless of assessed foot dominance. Participants were seated in a comfortable position with their left foot resting on a stool (Fig. 6.1), and were asked to remain as still as possible throughout each experimental block. On each trial, participants were touched twice on the hairy skin or glabrous skin of the left foot, once with the posts oriented along the proximodistal axis of the hand (along stimulus), and once oriented along the mediolateral axis (across stimulus). Stimuli used were the same as in Experiment 1 and 2.

Participants were randomly assigned to one of two groups, testing either the hairy or glabrous skin surface of the foot. Participants completed two blocks of 100 trials each, resulting in a total of 200 trials, and 40 trials for each of the five stimulus pairings (across/along): 20/40 mm, 20/30 mm, 30/30 mm, 30/20 mm, and 40/20 mm. This is the same number of trials as completed for one skin surface in Experiment 1. The order of along and across stimuli were counterbalanced within each stimulus pair, and order of trials randomised and shown the experimenter through a custom MATLAB script.

Analysis

Analyses closely followed Experiment 1 and 2. One participant tested on the glabrous skin had an R^2 value below 0.5, and was therefore excluded from the analysis. Of the remaining participants, R^2 values ranged from 0.92 to 1 ($M = 0.98$, $SD = 0.02$) on the hairy skin and 0.84 to 1 ($M = 0.96$, $SD = 0.04$) on the glabrous skin, indicating good fit of the data.

Initially, we investigated whether there are anisotropies in tactile distance perception on the two skin surfaces of the foot. We conducted two one-sample t-tests comparing the PSEs on the hairy skin and glabrous skin of the foot to 1 (i.e. no bias in responding). We also investigated similarity of tactile distance perception across the hairy and glabrous skin of the foot, first by correlating PSE values across the two skin surfaces. We also carried out an independent-samples t-test between PSE values on the hairy and glabrous skin surfaces.

6.4.2. Results and Discussion

The mean PSE for the hairy skin of the foot was 0.86, significantly less than 1, $t(19) = -4.51$, $p < .001$, $d = -1.01$, indicating a bias to represent the foot as wider than it really is. Out of 20 participants, 16 showed this bias, in that PSEs for every participant except four were less than 1 (range = 0.67 – 1.15). This finding is very similar to the findings of Experiment 1 and 2, and results from previous studies on the hairy skin of the hand.

The mean PSE for the glabrous skin of the foot was 0.93, which was not significantly less than 1, $t(18) = -1.87$, $p = 0.08$, $d = -0.43$. Out of 19 participants, 12 showed a bias towards perceiving the foot as wider than it really is (range = 0.71 – 1.21). Although different to the results of Experiment 1 and 2, these results show a similarity to results found on the glabrous skin of the hand – there are anisotropies in tactile distance perception, but these are reduced or non-significant compared to the hairy skin surface of the hand.

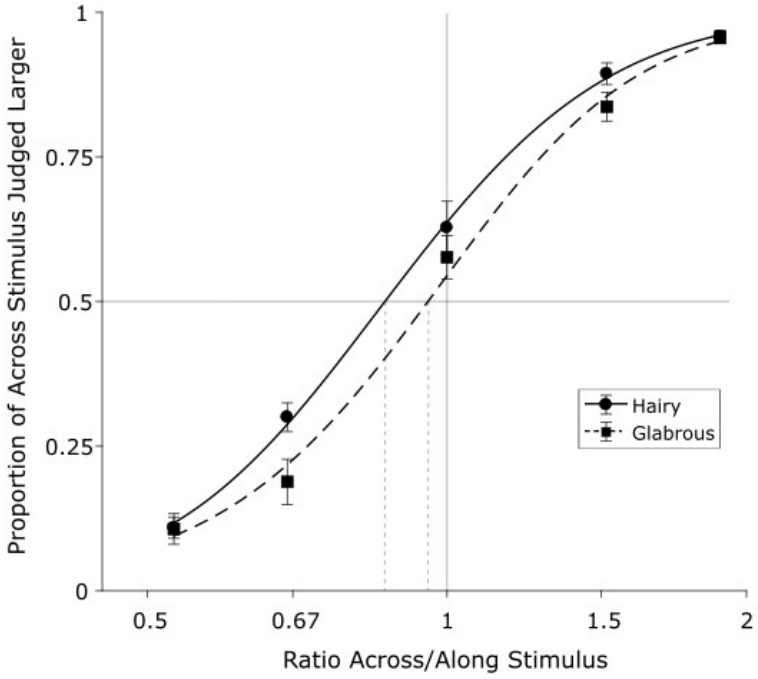

Figure 6.5. Results from Experiment 3. The curves are cumulative Gaussian functions fit with maximum-likelihood estimation Error bars represent the standard error of the mean. The solid vertical line that crosses the x-axis at one represents the point of subjective equality (i.e., where the curve crosses 50%). The dashed vertical line represents the grand average PSE for both the hairy and glabrous skin surfaces. The x-axis is plotted with log-transformed stimulus ratios to create an equal distribution around the point of subjective equality. However, the value labels are actual ratios values, for ease of understanding as this is consistent with the reporting in text.

PSEs on the hairy and glabrous skin surfaces of the foot were not correlated, $r(19) = 0.26$, $p < 0.28$, and an independent-samples t-test confirmed that there was no significant difference between the PSE scores on the hairy and glabrous skin surfaces, $t(37) = -1.65$, $p = 0.11$, $d = -0.53$.

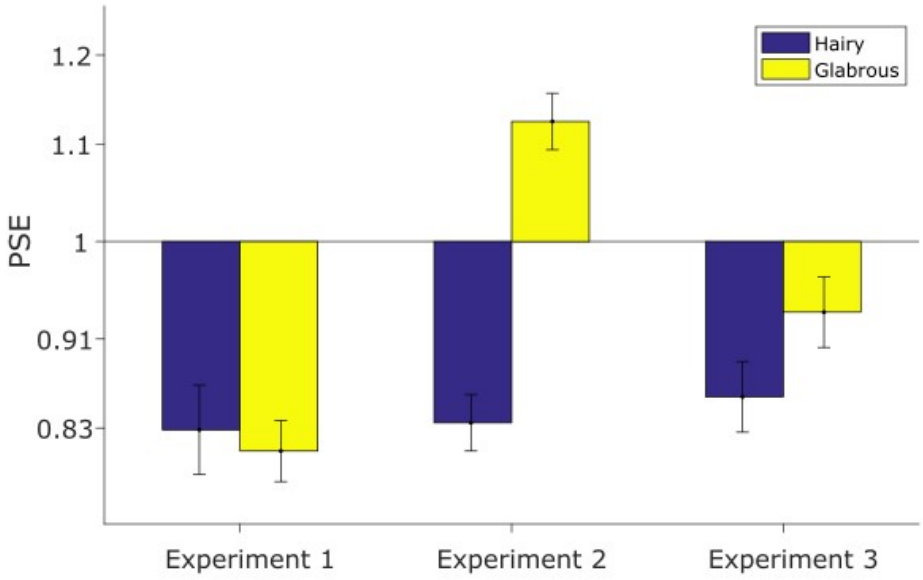

Figure 6.6. Results on the hairy and glabrous skin surfaces of the foot from the three experiments. The horizontal axis represents the point of subjective equality if there was no anisotropy (i.e., where 50% of stimuli are judged as larger).

6.5. General Discussion

In three experiments we investigated distortions in tactile size perception on the hairy and glabrous skin surfaces of the feet (Experiments 1, 2, and 3) and hands (Experiment 2). We replicated previous findings on the hand – tactile distances are perceived as farther apart when going across the hairy skin surface of hand, as opposed to along (Longo, Ghosh, et al., 2015; Longo & Haggard, 2011), and these biases were reduced on the glabrous skin surface of the hand (Longo, Ghosh, et al., 2015). On the hairy skin surface of the foot, we found consistent biases across Experiments 1, 2, and 3, to perceive tactile distances are father apart when going across the foot than along, consistent with results on the hairy skin surface of the hand.

The three experiments yielded different results for the glabrous skin surface of the foot, however. Experiment 1 showed anisotropies in tactile size perception

consistent in magnitude on the hairy skin surface of the foot, in contrast to findings of reduced tactile biases on the glabrous skin surface of the hand (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015). Anisotropies in Experiment 2 showed a bias towards perceiving tactile distances are farther apart when going along the foot, as opposed to across, in contrast to findings on a number of body parts that have been tested (Fiori & Longo, 2018; Green, 1982; Longo, Ghosh, et al., 2015; Longo & Haggard, 2011; Stone et al., 2018). Experiment 3 again showed that tactile distances were perceived as farther apart when going across the foot than along, although the magnitude of bias was reduced compared to the hairy skin surface of the foot, consistent with some findings on the hand (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015).

One possible explanation of the contradictory findings in the three experiments is that there were carryover effects between the different skin surfaces tested in Experiment 1 and 2. In Experiment 1, blocks in which the hairy and glabrous skin surfaces of the foot were tested were interleaved, possibly resulting in biases on the glabrous skin surface of the foot increasing in magnitude. Moreover, PSE on the hairy and glabrous skin surfaces of the foot were strongly correlated in Experiment 1, unlike in previous studies of the hand (Longo, Ghosh, et al., 2015), further suggesting that there may have been carryover effects. In Experiment 2, blocks testing the two skin surfaces of the hands and feet were also interleaved. None of the skin surfaces or body parts tested other than the glabrous skin of the foot appeared inconsistent with previous or expected results, however, if participants were less sure of responses on the glabrous skin surface of the foot (potentially as a result of reduced tactile acuity on the glabrous skin of the foot; Kennedy & Inglis, 2002), carryover effects may have caused confusion

in their responding. In Experiment 3, we carried out testing using the same methods as Experiment 1, but with separate groups tested on the hairy and glabrous skin surfaces of the foot. Using separate groups yielded results consistent with results previously found on the two skin surfaces of the hands (Longo, Ghosh, et al., 2015) – tactile distances were perceived as farther apart going across than along the foot, although magnitude of bias was reduced when compared to the hairy skin surface of the foot. These results suggest that anisotropies in tactile size perception are a general characteristic of the limbs.

This series of studies also provides further support to the pixel model proposed by Longo and Haggard (2011). According to the pixel model tactile space consists of a 2D array in which individual RFs form the pixels. Perceived size is measured by the number of 'pixels' (RFs) between two stimulated locations. For all skin surfaces tested (except the glabrous skin surface of the foot in Experiment 2), distances were perceived as greater when oriented across the body part than along. Magnitude of anisotropies were greater on the hairy than glabrous skin surfaces of both the hands (Experiment 2) and feet (Experiment 3), consistent with more distinctly oval-shaped RFs on the hairy skin surface (Alloway et al., 1989; Brooks et al., 1961), resulting in a greater number of 'pixels' counted between two points oriented across the hand, than along the hand. On the glabrous skin surface of the hands and feet, magnitude of anisotropies were smaller, as RFs are generally smaller and less elongated than on the hairy skin (DiCarlo & Johnson, 2002; DiCarlo et al., 1998), so the number of 'pixels' counted is equal for each stimulus orientation. However, there is some evidence to suggest that RFs on the glabrous skin surface of the feet are much larger and more randomly distributed than on

the hand (Kennedy & Inglis, 2002). This may provide an additional explanation for the inconsistency of our results on the glabrous skin surface of the foot across the three experiments presented here, in that RF distribution on the glabrous skin of the foot is also less consistent across the individuals tested than on the glabrous skin of the hand. Moreover, the reduced precision of RFs on the glabrous skin surface of the foot may be a reason why we find reduced, but not non-existent biases, such as have been found in some studies for the glabrous skin surface of the hand (Longo & Golubova, 2017; Longo & Haggard, 2011).

RFs on the palm of the hand are likely smaller and less elongated than on the dorsum of the hand as this increases spatial acuity, which is needed for skilled goal directed actions such as haptic object manipulation. Accurate size perception on the glabrous skin surface of the hand is one way that we can carry out such skilled actions. In contrast, the feet are not used to perform as many actions related to object manipulation as the hands, and spatial acuity of the RFs is lower than on the glabrous skin of the foot than the hand (Kennedy & Inglis, 2002). This may be reflected in our results of Experiment 1 and 3, which found anisotropies of the same or slightly lower magnitude as found on the hairy skin of the foot (but not non-existent). This further suggests that it is skilled actions such as haptic object manipulation, not simply contact or movement on the skin surface (such as is made on the foot while walking), that drives this difference in RF structure. This theory raises some interesting questions about how differences in RF structure develops – that it is related to the differences in use of the hands and feet in modern humans suggests that it is not solely related to the co-development of the limbs (Rolian et al., 2010). RF structure instead may change

throughout development with learning skilled use of the hands, or the feet, such as by congenital one-handers (Hahamy et al., 2017).

Together these results suggest that anisotropies in tactile size perception are a general characteristic of the representations of the limbs, as consistent results are found across both skin surfaces of the hands and feet.

Chapter 7: The one-way influence of double simultaneous stimulation on touch detection on the fingers and toes

7.1. Introduction

Our ability to detect touch on the body is a fundamental function of the somatosensory system. A method that has frequently been used to investigate how we detect touch on the body, and what this can tell us about the organisation of somatosensory body representations, is double simultaneous stimulation (DSS). In one study Tamè et al. (2011) used DSS to investigate the representational structure of the left and right hands. In the experiment participants were asked to respond on each trial any time they felt a tactile stimulus applied to a specified digit (the index or middle finger on the left or right hands). On some trials stimulation was applied to the target only, but on others stimuli were also applied to another digit simultaneously to the target. They measured reaction time and error rate of responses, and compared how these differed when different combinations of digits were stimulated – non-homologous fingers on the same hand, homologous fingers on the different hands, or non-homologous fingers on the different hands.

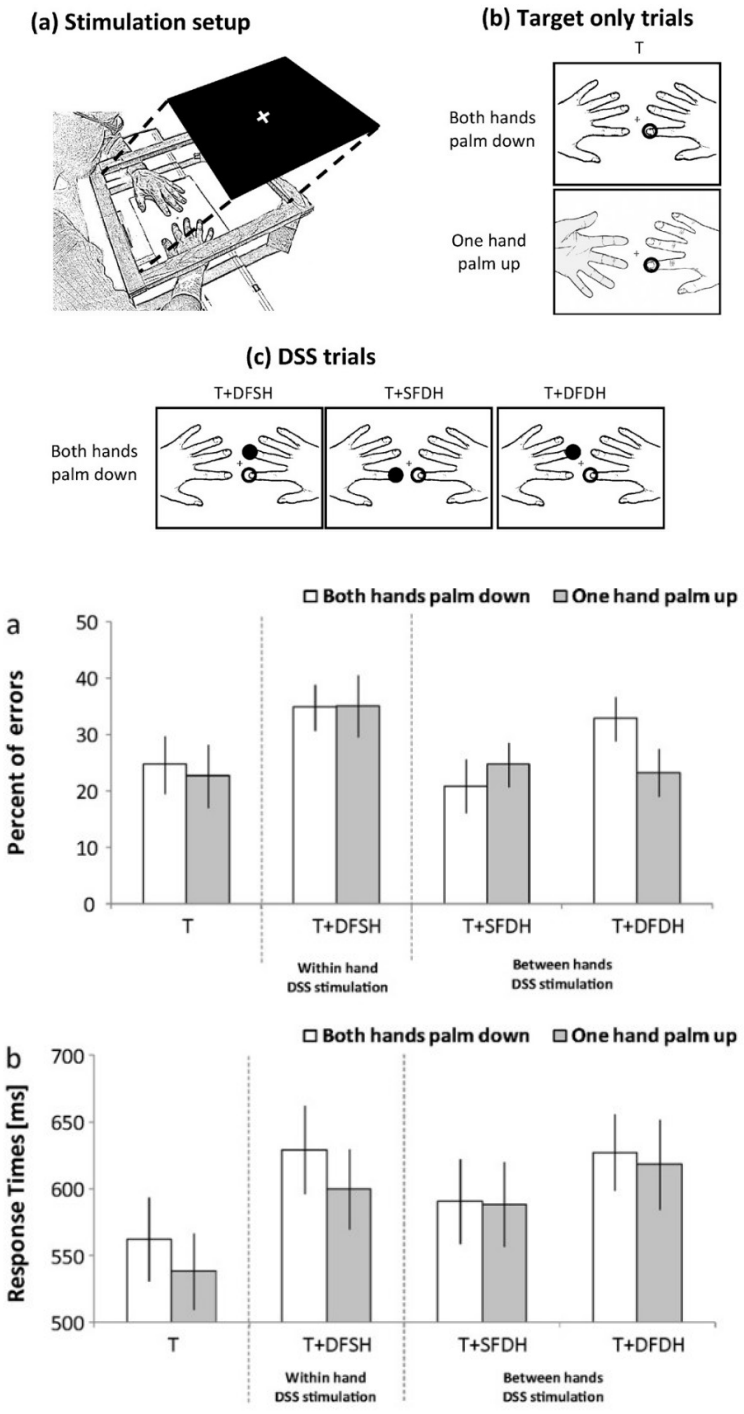

Figure 7.1. Results from Tamè et al. (2011). The upper panel shows the possible combinations of fingers stimulated on any trial (one hand palm up condition is not relevant to this study). When the target alone is stimulated (T), when target plus different finger on the same hand is stimulated (T+DFSH), when target plus same finger on different hand is stimulated (T+SFDH), and when target plus different finger on

different hand is stimulated (T+DFDH). The two graphs show the characteristic patterns of for percentage of errors and response times (error bars represent standard error of the mean). Distractor stimuli applied to the non-homologous digit on both the same and different hand comparably increased reaction time and error rate of responses to the target stimuli.

In this study they found increases in both response time and error rate when non-homologous fingers of the same hand were stimulated (e.g. left index finger and left middle finger), perhaps reflecting partial overlapping of tactile receptive fields for adjacent fingers in the somatosensory cortex (Besle, Sánchez-Panchuelo, Bowtell, Francis, & Schluppeck, 2014; Tamè et al., 2011, 2013). Moreover, they found that these increases in response time and error rate were comparable when non-homologous fingers of the *other* hand were stimulated as well (e.g. left index finger and right middle finger). Tamè and colleagues (2011) propose that this finding suggests that at some level there is a somatotopic representation of the body that is shared between the left and right side of the body.

Like the way Tamè et al. (2011) describe the existence of a body representation that does not distinguish between body-sides, recent research has suggested that there is a common high-level representation of the hands and feet. The hands and feet are serially homologous structures that co-evolved (Rolian et al., 2010), resulting in a number of physical similarities, such as both having hairy and glabrous skin on their alternate sides (Marieb, 2012), and sharing a qualitatively similar structural plan (Owen, 1849/2008). On a psychological level, Gerstmann's syndrome produces both finger agnosia (Kinsbourne & Warrington, 1962) and toe agnosia (Mayer et al., 1999; Tucha et al., 1997), and similar patterns of tactile confusions have been reported on the hand and foot (Cicmil et al., 2016; Manser-Smith et al., 2018; Schweizer et al., 2000). Moreover,

individual differences in individuals' patterns of confusions between digits has been found to be shared between the fingers and toes (Manser-Smith et al., 2019).

The aim of this study is to investigate the extent to which DSS interference occurs between, as well as within, the digits of the hands and feet. We will do this using testing and analysis methods similar to Tamè et al. (2011). If DSS interference occurs in the same pattern between the digits of the hands and feet as between the left and right hand, this would provide further support to the idea that there is a shared high-level representation of these two body parts. All procedures, including sample size, exclusion criteria, and analysis plans were pre-registered on the Open Science Framework (osf.io/9gvwq).

7.2. Methods

Participants

The effects reported by Tamè and colleagues (2011) were strong, the main effects of Stimulation Condition having partial eta-squared values of 0.19 and 0.54 for response accuracy and RT, respectively. A power analysis using G*Power 3.1 (Faul et al., 2007) with the smaller of these effect sizes, an alpha value of 0.05, and power of 0.95, indicated 14 participants were required. As we may expect a weaker effect to occur between the digits of the hand and the foot, we aimed to recruit 20 participants.

We recruited 20 participants (12 female; mean age = 30.7; range = 21-50). All 20 participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean = 65.5, range = 20-100). All participants were also right-foot dominant, as assessed by the Waterloo Footedness Questionnaire (Elias, Bryden, &

Bulman-Fleming, 1998; mean = 56.5, range = 10-100). EHI and WFQ scores were not correlated across participants ($r = 0.37$, $p = 0.11$) All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

Stimuli

Tactile stimuli were delivered to the left index, left middle finger, left big toe or left second toe, by using four vibrators (Piezo System, QuaeroSys, Q220-A4-203YB model). Tactile stimulus was a 30 Hz sinusoidal wave fed into the stimulators for 10ms. As tactile sensitivity differs across the four digits tested (Manser-Smith et al., 2018; Schweizer et al., 2000; Weinstein, 1962), the absolute strength of the stimulus applied to each digit was allowed to vary, so that touches felt perceptually identical on each finger. Measuring what strength of stimulus felt perceptually similar to each participant was done at the start of each testing session. Stimuli of the same strengths were applied to each digit, and participants were asked if any of the touches felt weaker than any of the others. If the stimuli applied to any of the digits was reported as weaker, intensity for that digit was increased in a small increment, and then touches were applied to each of the four digits again. This was continued until the participant reported that the stimuli applied to each digit felt perceptually identical. The average intensity used on the two fingers was the same (intensity control of the stimuli were arbitrary values, so we do not know the exact force exerted on each finger). Intensity on the big toe was 5.32% stronger than on the fingers, and on the second toe was 7.01% stronger than the fingers.

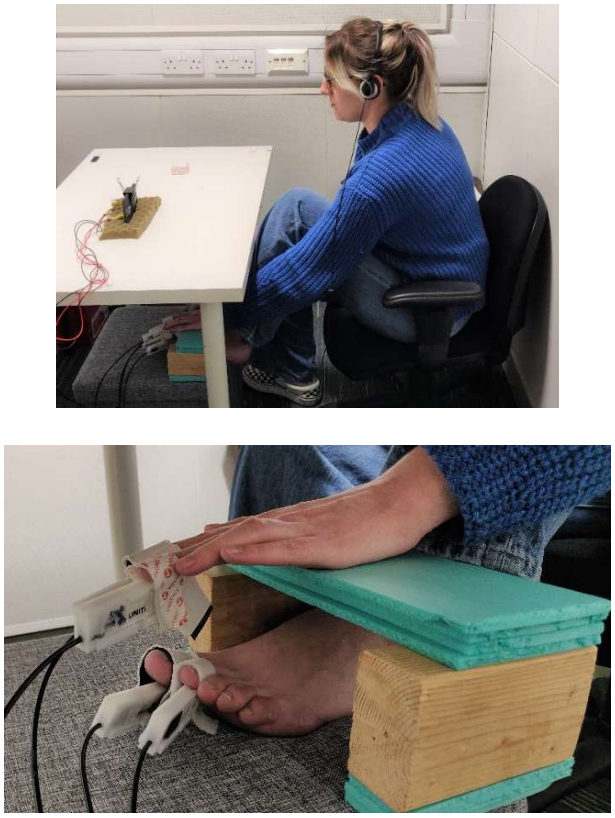

Figure 7.2. Experimental set-up. The left panel shows how the participant was seated. The left foot was resting on the edge of a stool, and their left hand resting on a foam board above the foot. Vision of the hand and foot was obscured by the table, upon which is the LED fixation light. The left panel shows the position of the hand and foot during testing. Stimulated fingers are placed above their analogous toes. No contact is made between the stimulators and the stool or foam board.

To maintain a homogeneous contact between the fingers and the vibrotactile stimulators, stimulators were secured to the fingers using Velcro strips that attached to the stimulator. Tactile stimuli were applied to the first and second toe, as opposed to the second and third toe (the homologous toes to the stimulated fingers), as during pilot testing participants reported difficulty in identifying which toe of the second or third was being stimulated. This is consistent with previous findings of tactile confusions between these toes (Manser-Smith et al., 2018). Moreover, research has indicated that there is a perceptual correspondence between the big toe and the index finger, as

opposed to the big toe and the thumb, so we could view these as perceptually analogous digits (Singh, 1990).

Task

The procedures were based on those used by Tamè and colleagues (2011). All participants were tested on their left hand and foot, regardless of assessed hand and foot dominance. Firstly, tactile stimulators were applied to the tip of the glabrous skin surface of the index finger, middle finger, big toe and second toe. Participants sat with their left foot resting on the edge of a stool, and their left hand resting on a foam board raised 15cm above the stool, to maintain a constant distance in external space between the fingers and toes. The stimulators did not make contact with either the stool or foam board to avoid carry-over stimulation between the digits. Stimulated fingers were placed above their analogous toes, and posture monitored by the experimenter throughout the block. Vision of the hand and foot was obscured by a table top.

There were eight blocks, two in which each of the stimulated digits was the "target". Order of the first four blocks (one for each target digit) was randomised at the start of the experiment for every participant, and this order reversed for the next four blocks. Each block contained 10 repetitions of each of the seven stimulation types, resulting in a total number of 70 trials per block, and 560 trials in total. Three stimulation types were DSS trials: target finger plus the neighbouring digit of the same body part ('T+DDSB trials', for Target + Different Digit Same Body-part); target digit plus the homologous digit of the other body part ('T+SDDB trials', for Target + Same Digit Different Body-part); or target digit plus the non-homologous digit of the other

body part ('T+DDDB trials', for Target + Different Digit Different Body-part). Three stimulation types were catch trials: 'DDSB trials', for Different Digit Same Body-part non-target; 'SDDB trials', for Same Digit Different Body-part non-target; and 'DDDB trials', for Different Digit Different Body-part non-target. Finally, there was target digit only (T-only) stimulation.

At the start of each block the participant was told which digit was the target for that block. Participants were asked to fixate on a light emitted diode (LED) embedded in a piece of black cardboard resting on the table top throughout the experiment. At the start of each trial the participant was cued to the onset of a tactile stimulation by the LED being on for a random time interval between 200 and 400ms. As soon as the LED turned off, the participant received a tactile stimulation on one or two of the digits. Participants were informed that their task was to perform a speeded go–no-go task to indicate whether the target finger had been stimulated or not. Specifically, they were instructed to keep the right foot-pedal pressed, unless they wanted to indicate the presence of a tactile stimulus at the target finger, when they lifted their foot off the pedal. Each trial did not start unless the foot pedal was pressed again. Participants wore headphones playing white noise during the experiment, to mask any noise produced by the Piezo stimulator.

Analysis

We computed the percentage of errors and reaction times (RTs) for T-only and DSS trials (T+DDSB, T+SDDB, and T+DDDB) for each target digit (big toe, second toe, index finger, and middle finger). We compared percentage of errors in each of these

conditions using a repeated-measures ANOVA with three factors: Digit (big toe/index finger, second toe/middle finger), Body Part (hand, foot) and Trial Type (T-only, T+DDSB, T+SDDB, T+DDDB). We carried out planned paired-samples t-tests between T-only trials and the three remaining Trial Types (T+DDSB, T+SDDB, T+DDDB). Bonferroni-Holm corrected post-hoc comparisons were carried out for significant interactions. We also carried out the same analyses with RTs as the dependent variable.

Errors in responding when the target finger was stimulated may occur in two scenarios: when the participant does not perceive the stimulation (detection errors), or when they perceive the stimulation on a different digit (localisation errors). As such we also analysed catch trials (DDSB, SDDB, and DDDB), as errors in these trials can only be localisation errors. Catch trials were analysed in a separate repeated-measures ANOVA with three factors: Digit (big toe/index finger, second toe/middle finger), Body Part (hand, foot) and Trial Type (DDSB, SDDB, DDDB).

The data was also analysed using signal detection theory (SDT). We used the d' (d-prime) index, to investigate differences in signal discriminability of the target stimuli across our conditions, that cannot be identified in analyses of percentage of error or RT. Moreover, we also used the c (criterion) index in order to assess the presence of any bias in the participants' responses. We carried out the same analyses as performed for percentage of error and RT, with d' and c as the dependent variables in separate ANOVAs. To compute d' and c values, we calculated the percentage of correct responses for T-only and DSS trials (T+DDSB, T+SDDB, and T+DDDB) for each target digit (big toe, second toe, index finger, and middle finger). Z-scores were

calculated for each participant, for each trial type and digit, and then transformed into d' and c values.

If DSS interference occurs between the digits of the hands and feet, we would expect to find that performance on T+DDSB and T+DDDB trials are significantly worse (higher percentage of errors, slower RTs and lower d' values) than T-only trials, but T+SDDB are not.

7.3. Results

Differences in RT for Fingers and Toes

Figure 7.3 shows the results of the three-way repeated-measures ANOVA on RT. There was a significant effect of Body Part, $F(1,19) = 4.93$, $p < 0.05$, $\eta_p^2 = 0.21$, but not of Trial Type or Digit (both $p > 0.05$), showing that responses to stimuli applied to the fingers were faster than those applied to the toes, regardless of trial type. Planned paired-samples t-tests confirmed that there were no differences in response times between T-only and all other target trials, T+DDSB: $t(19) = -0.01$, $p = 0.99$, $d = -0.003$; T+SDDB: $t(19) = -1.64$, $p = 0.12$, $d = -0.37$; T+DDDB: $t(19) = -0.82$, $p = 0.42$, $d = -0.18$.

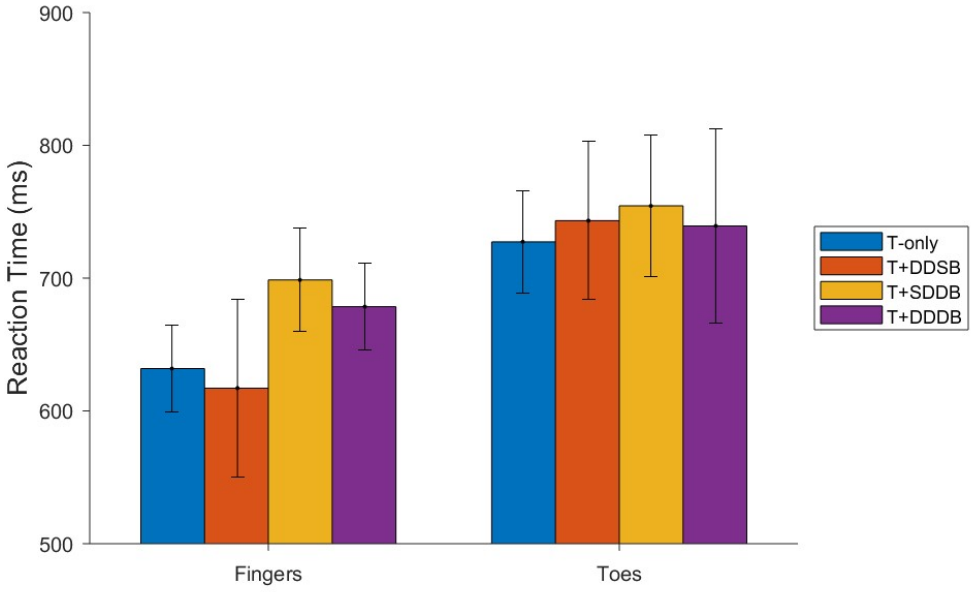

Figure 7.3. Results from the analysis of RT (ms). RTs were faster when the target digit was one of the fingers (index or middle) than one of the toes (big or second), for all trial types. Error bars represent standard error of the mean.

The analysis of RT does not indicate that there is any effect of DSS on tactile localisation of the fingers and toes. We failed to replicate the pattern of results reported by Tamè et al. (2011) for the fingers, that responses to T-only trials were significantly faster than all other trial types, and responses to T+SDDB trials were significantly faster than T+DDDB. Instead, despite altering the intensity of tactile stimuli to be on average stronger for the toes, participants were slower at localising touches to the toes. This may reflect the greater confusion in localising the individual toes than the individual fingers when an above threshold stimuli is applied (Cicmil et al., 2016; Manser-Smith et al., 2018).

Percentage of Error

Figure 7.4 shows the results of the three-way repeated-measures ANOVA with percentage of error as the dependent variable. We found significant effects of Trial Type ($F(3,57) = 18.22$, $p < 0.001$, $\eta_p^2 = 0.49$), and Body Part ($F(1,19) = 69.63$, $p < 0.001$, $\eta_p^2 = 0.79$), but not Digit ($p > 0.05$). We also found a significant three-way interaction between Trial Type, Body Part and Digit, $F(3,57) = 7.80$, $p < 0.001$, $\eta_p^2 = 0.29$.

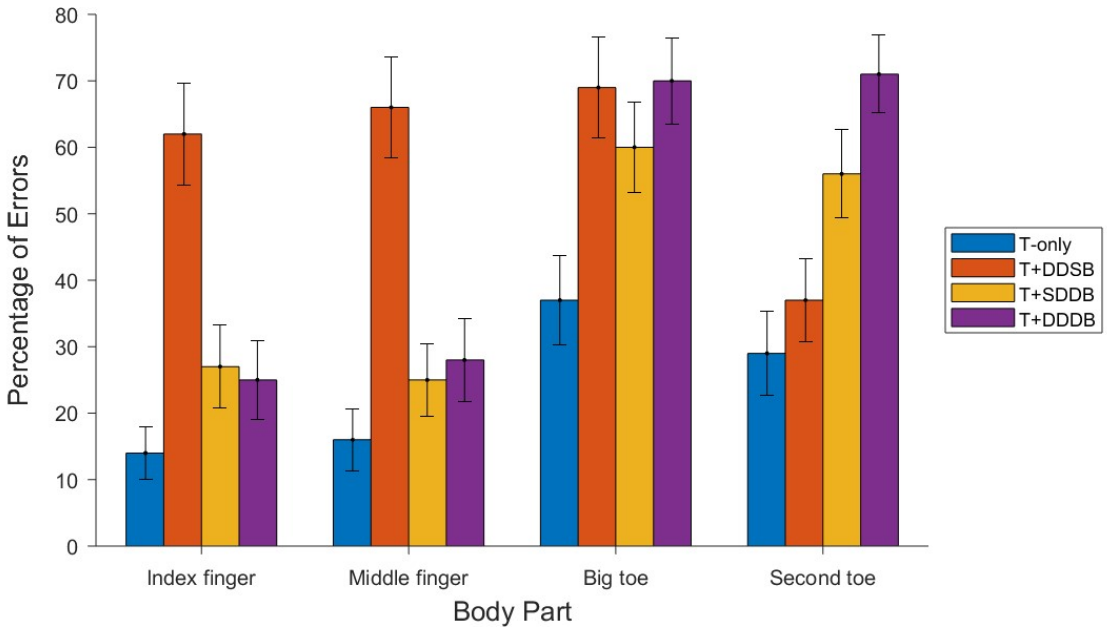

Figure 7.4. Results from the analysis of Percentage of Errors. For the fingers, DSS interference occurred only within, but not between, body parts (more errors only on T+DDSB trials). For the toes, distractor stimuli increased error rates compared to T-only trials regardless of whether the distractor was applied to the fingers or toes. Error bars represent standard error of the mean. Marked comparisons indicate significant differences ($p < 0.001$).

Bonferroni-corrected post-hoc comparisons indicated that when the index and middle fingers were targets, significantly more errors were made on T+DDSB trials than all other trial types (all $p < 0.001$). This indicates that there is an effect of DSS

interference for localising stimuli on the fingers, but only when the distractor stimulus is also applied to the fingers, but not when the distractor is applied to the toes.

When the target was the big toe, significantly fewer errors were made on T-only trials than all other trial types ($p < 0.001$). For the second toe, significantly fewer errors were made on T-only and T+DDSB trials than both T+SDDB and T+DDDB trials (all $p < 0.001$). These findings indicate that DSS interference occurs for localising stimuli on the toes when distracting stimuli is applied to either the fingers or toes, suggesting that the fingers may be treated as a more salient source of tactile information than the toes. One reason we may not find DSS interference between non-homologous digits on the same body part (as found in previous studies; Tamè et al., 2011) when the second toe is the target is that the big toe has the greatest tactile acuity of the toes (Manser-Smith et al., 2018, 2019), and therefore could easily be distinguished from touches to the second toe.

Planned paired samples t-tests showed that there were significant differences in error rate between T-only and all other target trials, T+DDSB: $t(19) = -6.03$, $p < 0.001$, $d = -1.35$; T+SDDB: $t(19) = -4.25$, $p < 0.001$, $d = -0.95$; T+DDDB: $t(19) = -4.64$, $p < 0.001$, $d = -1.04$. This contrasts with the findings of (Tamè et al., 2011), who found that T-only trials were only significantly different from T+DDSB and T+DDDB trials, for fingers. Our findings reflect the large effect found for the toes, that stimulation applied to *any* other digit at the same time as the target increases the number of errors made in detecting the target touch.

D-prime

Figure 7.5 shows the results of the repeated-measures ANOVA with d' as dependent variable. We found significant effects of Body Part ($F(1,19) = 71.62$, $p < 0.001$, $\eta_p^2 = 0.79$), Digit ($F(1,19) = 7.48$, $p < 0.05$, $\eta_p^2 = 0.28$) and Trial Type ($F(3,57) = 21.07$, $p < 0.001$, $\eta_p^2 = 0.53$). We also found a significant three-way interaction between Trial Type, Body Part and Digit, $F(3,57) = 12.49$, $p < 0.001$, $\eta_p^2 = 0.40$.

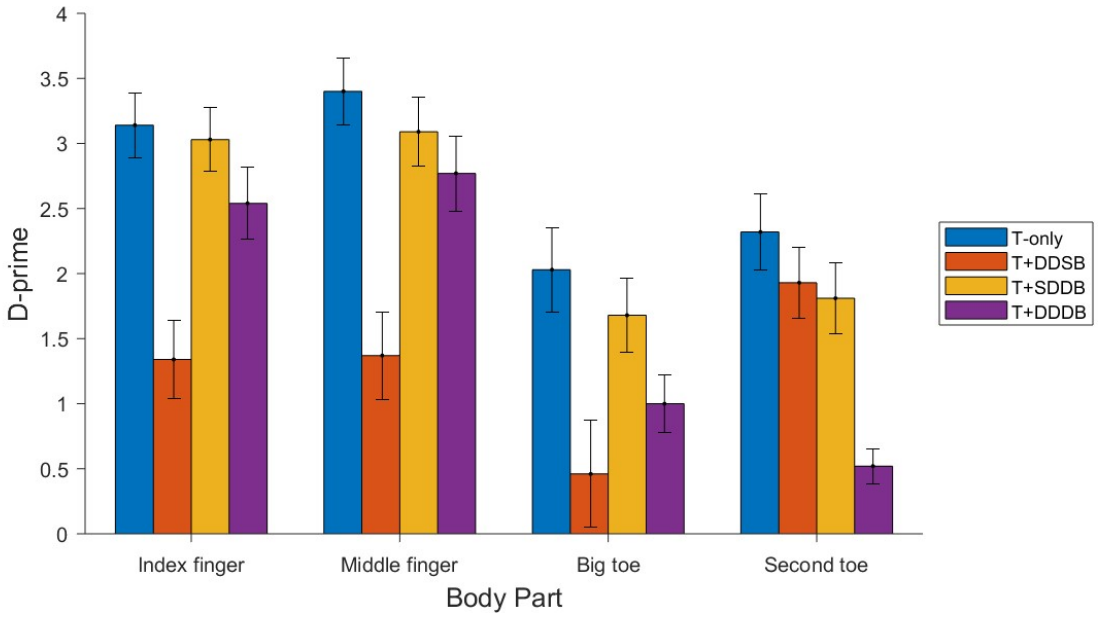

Figure 7.5. Results from the analysis of d'. For the fingers and the big toe, DSS interference occurred only within, but not between, body parts (lower d' values only on T+DDSB trials). For the second toe, DSS interference occurred only between, but not within, body parts (lower d' values only on T+DDDB trials). Error bars represent standard error of the mean. Marked comparisons indicate significant differences ($p < 0.001$).

Post-hoc comparisons indicated that when the index and middle fingers were targets, d' values were significantly lower for T+DDSB trials than all other trial types (all $p < 0.001$), reflecting worse ability to detect the target stimuli in this condition. This is consistent from our findings for the fingers of percentage of error, indicating that DSS

interference occurs only for the fingers when the distractor is also applied to the fingers, but not the toes.

When the big toe was the target, T+DDSB trials had significantly lower d' values than T-only and T+SDDB trials (all $p < 0.001$), indicating that as for the fingers, DSS interference occurred within the body part, but not between body parts. When the second toe was the target, T+DDDB trials had significantly lower d' values than all other trial types (all $p < 0.001$), indicating that for the second toe, DSS interference occurred between body parts but not within the body part. As mentioned previously, this perhaps reflects that the big toe has the greatest tactile acuity of the toes (Manser-Smith et al., 2018, 2019), and therefore could easily be distinguished from touches to the second toe.

Planned paired samples t-tests showed that d' scores were significant higher for T+DDSB trials and T+DDDB than T-only trials, $t(19) = 6.45$, $p < 0.001$, $d = 1.44$ and $t(19) = 4.48$, $p < 0.001$, $d = 1.00$, respectively. T-only and T+SDDB trials were not significantly different from each other, $t(19) = 1.54$, $p = 0.14$, $d = 0.34$. This replicates the characteristic pattern of DSS interference reported by (Tamè et al., 2011) between the left and right hands, and shows that this tactile interference also occurs between the hands and feet. Specifically, participants were worse at detecting the target stimuli when distractor stimuli were applied to the non-homologous digit of either the hand *or* foot. This indicates that there may be a single common representation of the hand and foot, and from this representation tactile mislocalisations may be made to 'neighbouring' digits (in the relative positions of the digits of both the hand and foot).

Criterion

Figure 7.6 shows the results of the three-way repeated-measures ANOVA with the criterion as the dependent variable. We found significant effects of Body Part ($F(1,19) = 17.22$, $p < 0.001$, $\eta_p^2 = 0.48$) and Trial Type ($F(3,57) = 20.23$, $p < 0.001$, $\eta_p^2 = 0.52$), but not Digit ($p > 0.05$). We also found a significant three-way interaction between Trial Type, Body Part and Digit, $F(3,57) = 6.61$, $p < 0.001$, $\eta_p^2 = 0.26$.

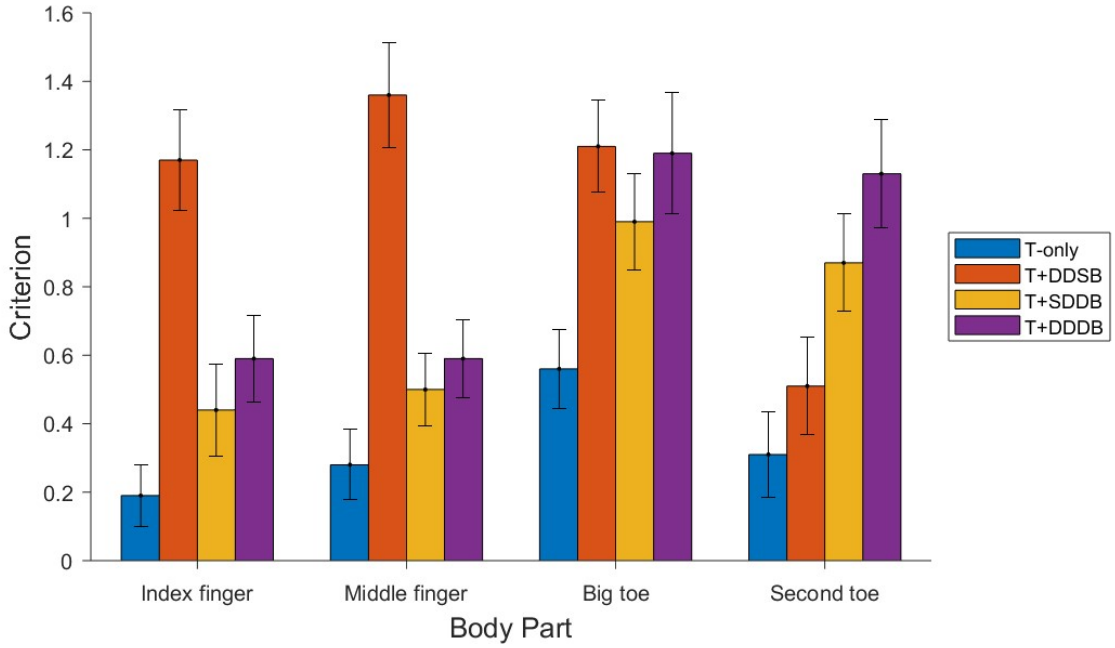

Figure 7.6. Results from the analysis of criterion. For the fingers, response biases differed only within, but not between, body parts (criterion higher only on T+DDSB trials). For the toes, distractor stimuli increased criterion scores compared to T-only trials regardless of whether the distractor was applied to the fingers or toes. Error bars represent standard error of the mean. Marked comparisons indicate significant differences ($p < 0.001$).

Post-hoc comparisons indicated that when the index and middle fingers were targets, criterion was significantly greater for T+DDSB trials than all other trial types (all $p < 0.001$). This suggests that participants had different response biases when the

distractor stimuli were presented on another finger of the hand, than when stimuli were presented only on the target, or either of the toes. This further suggests that distractor stimuli applied to the toes are not treated as salient information compared to touch on the fingers, as criterion was comparable for these conditions to when only the target stimuli was applied to the fingers.

When the big toe was the target, criterion scores were significantly lower for T-only trials than all other trials (all $p < 0.001$). This suggests that participants had different response biases for trials in which only the target was stimulated, as may be expected, as these trials are clearly different to other trials where two stimuli were presented. For the second toe, criterion values were lower for T-only and T+DDSB trials than both T+SDDB and T+DDDB trials (all $p < 0.001$). This suggests that participants' response biases were not different when a distractor stimuli was applied to the big toe than when only the target was stimulated, which is reflected in percentage of errors and d' values being consistent across T-only and T+DDSB trials when the second toe was the target.

Planned paired-samples t-tests showed that across the digits, T-only trials were significantly different from all other target trials, T+DDSB: $t(19) = -6.46$, $p < 0.001$, $d = -1.45$; T+SDDB: $t(19) = -4.33$, $p < 0.001$, $d = -0.97$; T+DDDB: $t(19) = -4.42$, $p < 0.001$, $d = -0.99$.

Catch Trials

In order to distinguish between types of errors made, we analysed percentage of errors made on the catch trials. As catch trials do not stimulate the target digit, errors

made on them can only reflect localisation errors, not detection errors. Results of the three-way repeated-measures ANOVA can be seen in Figure 7.7. We found significant effects of Body Part ($F(1,19) = 10.03$, $p < 0.01$, $\eta_p^2 = 0.35$) and Trial Type ($F(3,57) = 13.88$, $p < 0.001$, $\eta_p^2 = 0.42$), but not Digit ($p > 0.05$). We also found a significant three-way interaction between Trial Type, Body Part and Digit, $F(3,57) = 5.82$, $p < 0.01$, $\eta_p^2 = 0.23$.

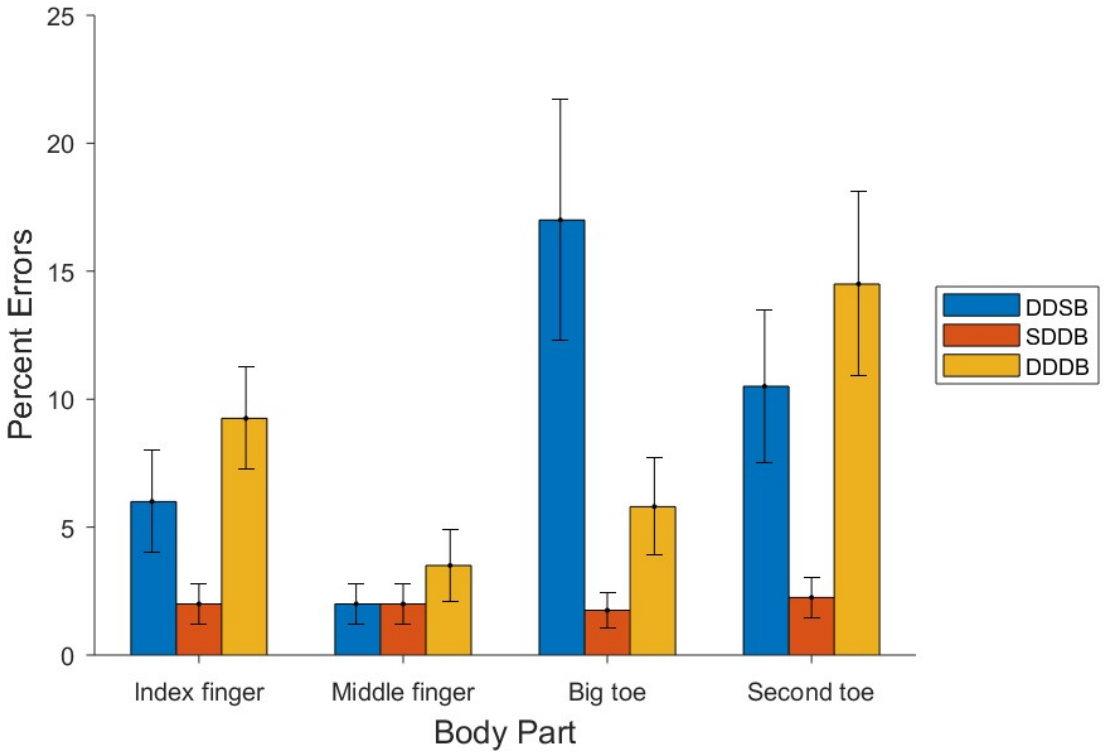

Figure 7.7. Results from the analysis of percentage of error for catch trials. When the non-homologous digit to the target digit was stimulated, either on the same or different body part, a larger number of errors were made than when the homologous digit was stimulated on the different body part. Error bars represent standard error of the mean. Marked comparisons indicate significant differences ($p < 0.001$).

Post-hoc comparisons indicated that for the index finger, significantly fewer errors were made on SDDB trials than DDDB trials ($p < 0.001$). No trial types were

significantly different for the middle finger. For the big toe, significantly fewer errors were made on SDDB trials than DDSB trials ($p < 0.01$), and for the second toe, fewer errors were made on SDDB trials than both DDSB and DDDB trials (both $p < 0.01$). These results reflect that for all digits except the middle finger, when a non-homologous digit to the target digit was stimulated (regardless of whether it was on the same or different body part to the target), more localisation errors were made than when the homologous digit on the other body part was stimulated. This finding tells us that errors made in T+DDDB trials are not detection errors but localisation errors, and so provides further evidence that there is a single common representation of the hand and foot, from which tactile mislocalisations are made to 'neighbouring' digits.

7.4. Discussion

In this study we investigated whether DSS interference occurs between, as well as within, the digits of the hands and feet. Like Tamè et al. (2011) we found that stimulation of the non-homologous finger on the same hand as the target increases error rate of responses, as well as reducing ability to detect the target stimuli. However, distractor stimuli applied to the toes did not interfere with peoples' ability to accurately detect touches to the target finger – participants response patterns did not differ from trials in which only the target was stimulated and trials in which the target and either toe was stimulated.

On the toes we found the opposite pattern of results – when attempting to detect touches on the big toe distractor stimuli applied to any other digit, whether fingers or toes, resulted in a greater number of errors than for target only trials. Participants

responded differently on target-only trials compared to all other trial types, suggesting that any distracting stimuli alters participants ability to detect touch on the big toe. However, analysis of d' reflected that participants are only worse at detecting target stimuli on the toes when distractor stimuli were applied to the non-homologous digit on the same body part (the same as for the fingers). This suggests that response errors made when distractor stimuli were applied to the fingers were not a result of poor ability to *detect* the target stimuli on the toes. Instead, response errors when distractor stimuli are applied to the fingers may arise at a later stage of somatosensory processing, or decision-making processing, perhaps involving weighing the saliency of the tactile information.

When detecting touches applied to the second toe, participants made a large number of errors only when distractor stimuli were applied to either of the fingers, but not the big toe. Analysis of criterion indicated that participants responded differently when distractor stimuli were applied to the fingers than when the target only was stimulated, or the big toe was the distractor. In fact, participants were only worse at detecting touches on the second toe when the index finger was stimulated (non-homologous digit on the other body part). This finding seems to suggest that participants found it difficult to detect touch on the second toe only when the index finger was stimulated. This may in fact be the case – in the characteristic pattern of DSS interference described by Tamè et al. (2011) distractor touches on the homologous digit of the other body part are easily distinguishable from the target (i.e. the second toe and middle finger in the present experiment), but touches on the non-homologous digit of the other body part are not (i.e. the second toe and index finger). The pattern of results

we find for the second toe follow this pattern, although we do not also find the characteristic confusion of the two digits on the same body part. This may be because tactile acuity of the big toe is greater than that of the second toe (Manser-Smith et al., 2018, 2019), so touches to the big toe can easily be correctly localised and distinguished from the second toe. As such, in the present case, when a distractor stimulus is applied to the big toe while focusing attention on the second toe, the distractor stimulus is more easily correctly localised, resulting in fewer errors on these trials. In contrast, when a distractor stimulus is applied to the second toe while focusing attention on the big toe, the touch is not localised as accurately as for the big toe. This idea is further supported by the results from catch trials (Fig. 7.7) – fewer localisation errors were made on trials in which the big toe was stimulated (DDSB trials for the second toe) than when the second toe was stimulated (DDSB trials for the big toe), although the difference between these trial types was not significant ($p = 0.15$).

Altogether these findings suggest that there are some differences in how somatosensory information is treated for the fingers and toes. We found that when focusing on tactile stimuli applied to the fingers, participants could easily ignore distractor stimuli applied to the toes, but not the other finger. When focusing on tactile stimuli applied to the toes, however, participants' performance was affected by any distractor stimuli, whether on the fingers or other toe. This one-way relationship may reflect the different uses of the fingers and toes. Without even our conscious attention we use the hands and fingers to perform fine-grained motor actions such as grasping and manipulating objects, relying on constant somatosensory feedback to assess task requirements and update actions online (Bilaloglu et al., 2015; Hall, Karl, Thomas, &

Whishaw, 2014; Lukos, Choi, & Santello, 2013; Sacrey & Whishaw, 2012; Whitwell, Ganel, Byrne, & Goodale, 2015). For example, adjusting grip posture or tension to securely grasp an object. On the other hand, the toes are not used for actions like grasping (with the exception of congenital one-handers [Hahamy et al., 2017]), although they are used for skilled actions that require somatosensory feedback. For example, somatosensory feedback from the big toe specifically is important for stance, balance and locomotion (Chou et al., 2009; Hughes et al., 1990; McNutt et al., 2018; Rolian et al., 2009). However, the type of somatosensory information presented in this experiment is more commonly felt on the fingers than the toes, making the touches on the fingers potentially more salient and harder to ignore. As such, the different uses of the fingers and toes, and so the type of somatosensory information that is salient for their purposes, may influence how particular stimuli are treated.

We suggested in introducing this study that DSS interference occurring between the fingers and toes would provide evidence that there is a common representation of the fingers and toes. While we find that simultaneous touches to the fingers and toes can influence ability to detect touches on the toes, we do not find that it affects ability to detect touch on the fingers. However, we can still argue that the findings of this study provide evidence for a common representation of the fingers and toes. Analysis of catch trials suggests that difficulty in detecting touches on the non-homologous digit is a result of localisation errors, not detection errors. Localisation errors are somewhat common for neighbouring fingers (Manser-Smith et al., 2018; Schweizer et al., 2000) and toes (Cicmil et al., 2016; Manser-Smith et al., 2018), as the fingers and toes are sequentially organised from the first digit to the fifth in SI, with some overlap between the individual

digit representations (Besle et al., 2014; Disbrow et al., 2000; Kolasinski et al., 2016; Martuzzi et al., 2014). However, localisation errors for 'neighbouring' digits on *different* body parts must arise from a common representation of the two body parts.

Another possible reason why we find that there is a distracting effect of stimuli applied to the fingers when detecting touch on the toes but not vice versa is that selectivity in individual toe representation is lower than for the fingers (Akselrod et al., 2017), making it more difficult to differentiate the individual toes than the individual fingers. This may increase reliance on another representation of the toes, in this case the common representation with the fingers, in order to provide another point of reference for detecting the location of stimuli, although this also increases errors made between digits on the other body part. This furthers our understanding of the common representation of fingers and toes, suggesting that reliance on this representation may depend on specific task demands.

We do not manage to replicate the pattern of DSS interference found by (Tamè et al., 2011) for RT. They found a comparable slowing of responses on trials in which the non-homologous digit of the same hand and the other hand were stimulated with the target, compared to target-only trials and trials in which the homologous digit was stimulated with the target. We found that RTs were faster for the fingers than the toes in all conditions, despite the fact that for most participants we applied a stronger tactile stimulus to the toes than to the fingers. The effects on RT reported by Tamè and colleagues was in some part driven by a large difference in RT between target-only trials and all other trial types, suggesting that the effect of DSS interference on RT may be weaker than other measures anyway.

In this experiment we showed that there is a one-way influence of DSS on touch detection for the fingers and toes. When detecting touches on the fingers, only concurrent stimulation of the non-homologous finger reduced participants' ability to detect a touch on the target digit. For the toes, however, concurrent touches to any digit and the target reduced participants' ability to detect touch on the toes. We suggest that patterns of usage of the fingers and toes may drive this difference, in that single touches such as given in this experiment are more salient information for the fingers than the toes. Moreover, these findings further support the idea of a common representation of the fingers and toes – comparable localisation errors are made on trials when the non-homologous digit of the same body part and the *other* body part are stimulated, suggesting that they arise from a single representation.

Chapter 8: Fingers hold spatial information that toes do not

8.1. Introduction

There are striking similarities between the hand and foot: they are serially homologous (Rolian, Lieberman, & Hallgrímsson, 2010), both have hairy and glabrous skin on their alternate sides (Marieb, 2012), and share a qualitatively similar structural plan (Owen, 1849/2008). Yet they also have important differences. The bones of the hands and feet differ considerably in size and shape (Marieb, 2012), and the nature of the mechanoreceptors on the two body parts differs (Kennedy & Inglis, 2002). Most obviously there are dramatic differences in the patterns of usage between the hand and foot in our everyday activities. At a psychological level, there are hints in the literature that there may be deep functional connections between the mental representations of the hands and feet. For example, Gerstmann's syndrome produces both finger agnosia (Kinsbourne & Warrington, 1962) and toe agnosia (Mayer et al., 1999; Tucha, Steup, Smely, & Lange, 1997). Moreover, similar patterns of tactile confusions have been reported on the hand and foot (Cicmil et al., 2016; Manser-Smith et al., 2018; Schweizer et al., 2000). Here, we investigated whether the hands and feet also share common associations between body parts and spatial locations.

There is a large body of evidence showing that tactile perception is modulated by specific body postures. For example, crossing the hands over the body midline reduces our efficiency in localising touch on the body (Yamamoto & Kitazawa, 2001), as does crossing the feet (Schicke & Röder, 2006), and crossing the fingers (de Haan et al., 2012). Romano, Marini, and Maravita (2017) have developed a novel method for

measuring such associations between body parts and spatial locations. They found that participants responded to tactile stimulation faster when it was applied to the thumb when it was in a relative *bottom* position than top position, and responded faster to the index finger when it was in a relatively *top* position than bottom position. In a recent follow-up study Romano and colleagues (2019) showed that all four fingers have preferential associations with a relative top position, suggesting that the canonical posture of the hand is configured like a pair of pliers. They describe these preferential associations between body parts and spatial locations as standard representations of body-space relationships. Such standard representations may be embedded into body representation and facilitate efficient localisation of tactile stimuli independent of ongoing postural changes.

How these standard representations emerge is not clear. One possibility is that they are general features of how the limbs are represented. Human hands and feet are serially homologous structures that co-evolved (Rolian et al., 2010), and so share a number of similarities such as those described previously. Shared standard body-space representations between the hands and feet may also be a product of this co-development. In particular for our close non-human primate relatives such as chimpanzees, that use both their hands and feet for dextrous actions such as grasping (Holowka, O'Neill, Thompson, & Demes, 2017b; 2017a), it would be equally evolutionarily advantageous for hands and feet to have standard representations. However, as human hands and feet now have widely different uses, it is not clear whether standard associations would be conserved for the toes.

Another possibility is that standard body-space relationships are learned from frequent actions or postures, reflecting the statistics of natural hand usage. Natural use relationships have already been shown to be related to other somatosensory functions, such as transfer of tactile learning between fingers (Dempsey-Jones et al., 2016) and the representational structure of sensorimotor cortex (Ejaz et al., 2015). Given the fundamentally different patterns of usage between hands and feet in humans, we might expect the hands and feet to have different patterns of spatial association.

The present study investigated whether standard body-space relationships, such as have been found for the hand, are also present in the feet. By using a method closely modelled on Romano and colleagues (Romano et al., 2017), we aimed to investigate to what extent the toes have similar preferential body-space associations to the fingers. If there were similarities in standard body-space associations between these two body parts, this would provide evidence that standard representations are general features of the representation of the limbs. If we found that they were not similar, this would suggest that standard representations are learned from natural hand usage.

8.2. Methods

Participants

The effects reported by Romano and colleagues (2017) were very strong – the critical interaction between stimulated digit and location (indicating that responses differed to the two digits in different locations) having partial eta-squared values of 0.80 and 0.83 in two experiments. A power analysis using G*Power 3.1 (Faul et al., 2007) with the smaller of these effect sizes, an alpha value of 0.05, and power of 0.95,

indicated six participants were required. We aimed for 20 participants, but ended up with one extra. As such, our experiment is appropriately powered to replicate the basic effect of Romano and colleagues on the hands, and investigate the presence of the same effect on the feet.

Twenty-one individuals participated (8 female, mean age = 33 years). All reported normal touch and gave written informed consent. Twenty were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean = 73) and all were right-foot dominant as assessed by the Waterloo Footedness Questionnaire (Elias, Bryden, & Bulman-Fleming, 1998; mean = 59). The study was approved by the Birkbeck Psychological Sciences ethics committee.

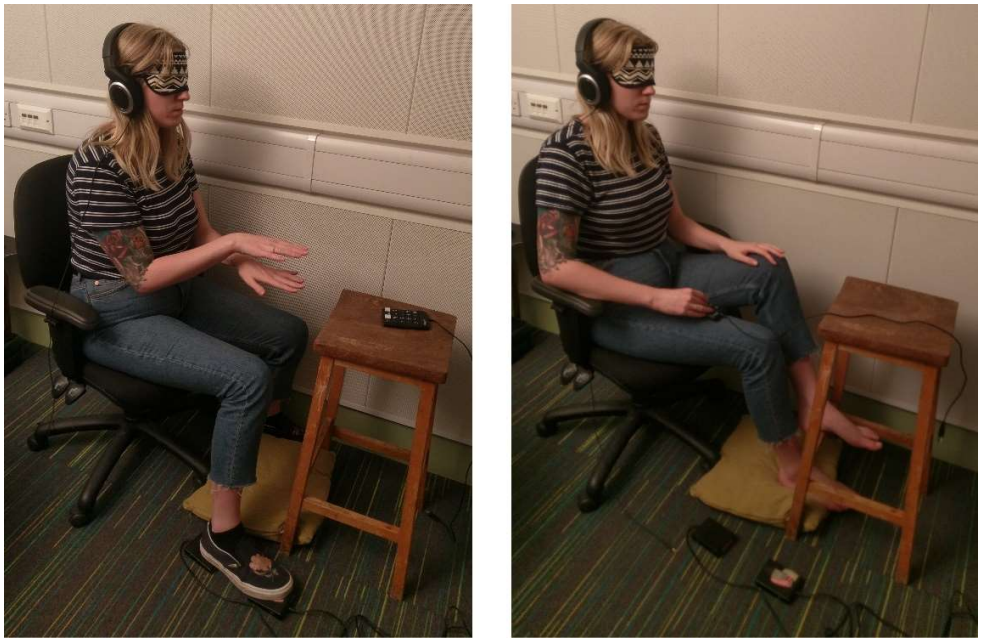

Figure 8.1. The left panel shows the posture held while testing the hands. The right panel shows the posture held while testing the feet. In both postures the hands/feet were held one above the other, without touching, in front and aligned with the body midline.

Task

Procedures were similar to Romano et al. (2017). Participants sat in a chair with tactile stimulators applied to the tip of the glabrous skin surface of the thumb and middle finger of both hands, or the tip of the glabrous skin surface of the big toe and third toe of the feet. The middle finger and third toe were used instead of the index finger and second toe, as pilot participants reported difficulty in distinguishing the big toe and second toe. This is consistent with previous findings of patterns of tactile confusions across the toes (Cicmil et al., 2016; Manser-Smith et al., 2018). On each trial the participant received a touch at one of four locations on the fingers or toes – first or middle digit, in the top or bottom position. They were asked to respond as quickly as possible by judging whether the stimulation occurred on a digit in the top or bottom position (regardless of which digit was stimulated or whether it was the left or right hand/foot).

Figure 8.1 shows the posture used for testing the hands (left panel) and the feet (right panel). The hands were held one above the other, without touching, in front of the body midline. The feet were also held one above the other, with the heel of the top foot resting on a stool to reduce fatigue. Participants were tested in the same postures, but with the left and right hand/foot positions reversed in half the blocks. The posture we used for the hands was different to that used by Romano et al. (2017; in press), wherein the thumb and index finger were positioned in two 'L' shapes, with the two thumbs and two index fingers positioned one above the other as if to form a square. As it was not possible for the feet to be held in the position they used a position was chosen that could

comfortably be held by both the hands and feet, as shown in Figure 8.1. Vision was occluded using a blindfold.

The experiment consisted of four blocks – in two blocks only the fingers of both hands were stimulated, and in two blocks only the toes were stimulated. Alternate participants started by performing either both hand or both foot blocks. Tactile stimulators could only be applied to either the fingers or the toes at one time (to allow responses to be made with the alternate body part), and was a time consuming process, so AABB counterbalancing was used to minimise the number of times changing the stimulator locations. There were two of each hand and foot blocks so that limb position could be varied between the blocks, eliminating the possibility of a left/right compatibility bias in responding. In one block the left limb was in the 'top' position and the right limb in the 'bottom' position, and in the second block the right limb was in the 'top' position and the left limb in the 'bottom' position. Order of the two hand or foot blocks was randomised for each participant. Each block contained 160 trials in random order, resulting in 640 trials per participant.

Apparatus and Stimuli

Tactile stimuli were delivered through four solenoid tactile stimulators (8 mm in diameter; M & E Solve, UK), controlled by a National Instruments I/O Box (NI USB-6341) driven using a custom MALTAB script (Mathworks, Natick, MA). Each stimulus consisted of a train of three 30ms stimuli interleaved with an off phase of 30ms, resulting in a vibro-tactile stimulation of 150ms.

When stimulation was applied to the hand, responses were collected using two foot-pedals – one below the toe and one below the heel of the right foot. Participants responded to the 'top' position by lifting the toe, and to the 'bottom' by lifting the heel. When tactile stimulation was applied to the toes, a number pad was used. Participants responded to the 'top' using their right middle finger, and 'bottom' using their right thumb. Stimulus-response compatibility bias (that responses using the toe of the foot and middle finger always corresponded to 'top' judgements, and using the heel and thumb always corresponded to 'down' judgements) are unlikely to influence pattern of results given the robust findings of Romano et al. (2017) using both the paradigm used in the present experiment and using an implicit association task (IAT). The IAT measured the strength of conceptual associations between body parts and spatial concepts using an association task – RTs were faster to images of index fingers when the word 'up' was present, and images of middle fingers when the word 'down' was present. These findings suggest that spatial associations are also present at the level of implicit conceptual associations.

Analysis

Analyses were modelled on those of Romano et al. (2017). RTs were trimmed to remove outliers, defined as trials faster than 200 ms (anticipatory responses) as well as trials exceeding three standard deviations above the individuals' mean (late responses; range = 440ms – 4750ms). Remaining responses were log-transformed to address the asymmetrical distribution of RT responses (Ratcliff, 1993). Accuracy scores were transformed using the arcsine of the square root, to align the distribution to meet the

assumptions of analyses of variance (ANOVA) (Zubin, 1935), as participants often scored at 100% accuracy.

We conducted repeated-measures ANOVAs with two factors: relative POSITION (top/bottom) and DIGIT (first/middle) receiving tactile stimulation. RTs and error rate were dependent variables in separate analyses. For each interaction, we carried out Bayesian repeated measures ANOVAs (Wetzels et al., 2012) to quantify evidence for or against the null hypothesis (H_0). Where BF_{01} (Bayes factor) was reported, this expressed the likelihood of H_0 relative to H_1 given the current data, and vice versa for BF_{10}. Bayesian statistics were carried out using JASP (version 0.8.2.0) with the default parameters.

We predicted faster and more accurate discrimination of tactile stimuli when the middle finger was in a relative top position than when it was in a relative bottom position, and vice versa for the thumb, as found by Romano et al (2017). This would be reflected in an interaction between the POSITION and DIGIT factors. If the toes also hold similar spatial information, then the same interaction should be present in the ANOVA on the toes. If standard postures were different for the fingers and toes, this would be evident in a significant interaction between BODY PART, POSITION and DIGIT. The data associated with this research are available through the Open Science Framework (OSF; osf.io/t4rnm).

8.3. Results

Fingers Hold Spatial Information

We started by analysing just the data from the fingers to compare our results to those of Romano and colleagues (2017). The left panel of Figure 8.2 shows RTs in each of the four conditions. An ANOVA showed a significant main effect of POSITION ($F(1,20) = 7.18$, $p = 0.01$, $\eta^2_p = 0.26$) and a nearly significant effect for DIGIT ($F(1,20) = 4.06$, $p = 0.06$, $\eta^2_p = 0.17$). Most critically, the interaction between POSITION and DIGIT was highly significant ($F(1,20) = 63.36$, $p < 0.0001$, $\eta^2_p = 0.76$). As can be seen in Figure 8.2, there was a clear crossover interaction. Follow-up tests showed that responses on the thumb were faster when it was in a relative bottom position than a relative top position (753.53 and 907.61 ms; $t(20) = 5.26$, $p < 0.001$, $d_z = 1.15$). Conversely, responses on the middle finger were faster when it was in a relative top than bottom position (692.71 and 933.67 ms; $t(20), = 7.36$, $p < 0.001$, $d_z = 1.61$). A Bayesian repeated-measures ANOVA revealed very strong evidence for the alternative against the null hypothesis for the interaction, $BF_{10} = 5.64 \times 10^{11}$.

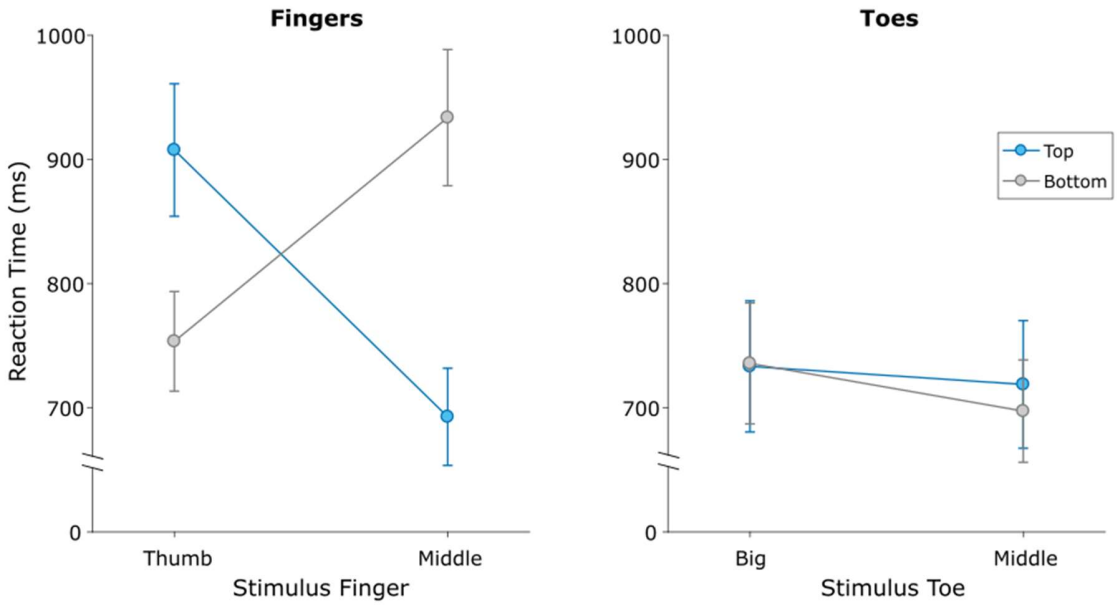

Figure 8.2. Grand average RTs for the fingers (left panel) and toes (right panel). Error bars represent standard error of the mean. Participants were considerably faster at responding to the fingers when the thumb was in a relative bottom position, and the middle finger in a relative top position, than vice versa. Participants were equally fast at responding to the toes in all locations.

The left panel of Figure 8.3 shows error rate in each of the four conditions. The ANOVA with error rate as dependent variable also showed a significant interaction between the two factors ($F(1,20) = 117.81$, $p < 0.001$, $\eta^2_p = 0.86$), while the two main effects were not significant (POSITION: $F(1,20) = 0.34$, $p = 0.57$, $\eta^2_p = 0.02$; DIGIT: $F(1,20) = 0.06$, $p = 0.80$, $\eta^2_p < 0.01$). Follow-up paired t-tests revealed that responses were more accurate on the thumb when it was in a relative bottom position (error rate ± standard error: 8.68% ± 2.66) than top position (22.40% ± 3.60; $t(20) = 9.61$, $p < 0.001$, $d_z = 2.10$). Again, responses to the middle finger were more accurate when it was in a relative top position (9.07% ± 3.61) than a relative bottom position (25.51% ± 5.74; $t(20) = 6.89$, $p < 0.001$, $d_z = 1.50$). A Bayesian repeated-measures ANOVA suggested

that there is very strong evidence for the alternative against the null hypothesis for the interaction, $BF_{10} = 1.23x10^{9}$.

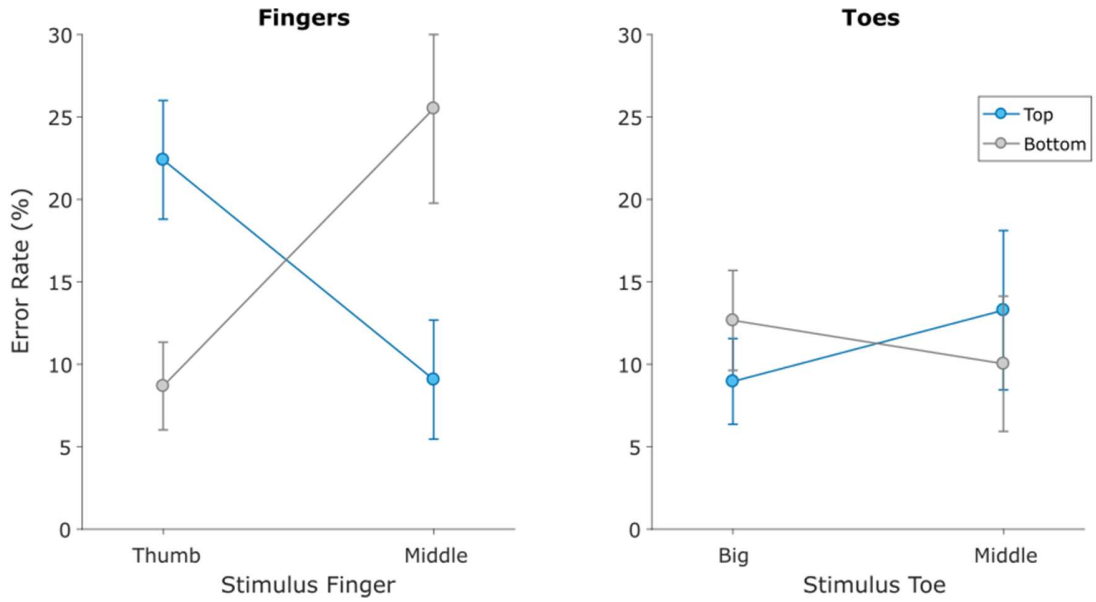

Figure 8.3. Grand average error rates for the fingers (left panel) and toes (right panel). Error bars represent standard error of the mean. Participants made considerably fewer errors in responding to the thumb when it was in a relative bottom position, and the middle finger in a relative top position, than vice versa. Participants made fewer errors overall when responding to the toes in all locations.

These results replicate the results of Romano and colleagues (in press) using the thumb and middle finger, that as well as being faster, responses were more accurate when the thumb was in the bottom position, and the middle finger in the top position, than vice versa. This further supports the conclusion that there are standard body-space relationships that facilitate responding to tactile stimuli.

Toes Do Not Hold the Same Spatial Information as Fingers

Our novel question was whether the toes also hold spatial information. The right panel of Figure 8.2 shows RTs for the toes. In contrast to the fingers, there was only a significant main effect of DIGIT ($F(1,20) = 10.82$, $p < 0.01$, $\eta^2_p = 0.35$). Responses to the middle toe were faster regardless of whether it was in the top or bottom (718.64 and 697.34 ms) position, compared to the big toe in the top or bottom position (733.36 and 735.65 ms). The main effect of POSITION ($F(1,20) = 0.05$, $p = 0.83$, $\eta^2_p < 0.01$) and the interaction between DIGIT and POSITION ($F(1,20) = 0.84$, $p = 0.37$, $\eta^2_p = 0.04$) were not significant. To further investigate the non-significant results of the interaction, we conducted a Bayesian repeated-measures ANOVA. The results indicated that there was weak evidence for the null over the alternative hypothesis, $BF_{01} = 2.16$.

The right panel of Figure 8.3 shows error rates for the toes. The ANOVA with error rate as the dependent variable showed a significant interaction ($F(1,20) = 5.64$, $p = 0.03$, $\eta^2 = 0.22$), but no significant main effect for either the factor POSITION ($F(1,20) = 0.49$, $p = 0.49$, $\eta^2_p = 0.02$) or DIGIT ($F(1,20) = 0.05$, $p = 0.82$, $\eta^2_p < 0.01$). The pattern of results on the toes was inverted from error rate on the fingers: responses were *less* accurate to the big toe when it was in a relative bottom position (12.66% ± 3.03) than top position (8.96% ± 2.60). Responses to the middle toe were also less accurate when it was in the top position (13.73% ± 4.83) than bottom position (10.03% ± 4.10). However, this difference was only significantly different between the middle toes ($t(20) = -2.663$, $p = 0.02$, $d_z = -0.58$), and not the big toes ($t(20) = 1.17$, $p = 0.26$, $d_z = 0.26$). A Bayesian repeated-measures ANOVA indicated that there was weak evidence for the alternative over the null hypothesis for the interaction, $BF_{10} = 1.17$.

These results indicate that while the toes may hold weak spatial information, this information is different to that held by the fingers. This suggests that standard body-space relationships of the digits are not only a general characteristic of the limbs, but are learned through actions and postures used by the hands, but not the feet.

Differences in Spatial Information Held by Fingers and Toes

To directly compare performance on the fingers and toes, we conducted a 2*2*2 ANOVA. There was a significant main effects of BODY PART ($F(1,20) = 7.50$, $p = 0.01$, $\eta^2_p = 0.27$), as well as a significant three-way interaction between POSITION, DIGIT, and BODY PART ($F(1,20) = 79.04$, $p < 0.0001$, $\eta^2_p = 0.80$). This three-way interaction verifies that the fingers and the toes hold different spatial information (these differences are described in the specific body part analyses).

A 2*2*2 ANOVA with error rates as the dependent variable again showed a significant effect of BODY PART ($F(1,20) = 6.62$, $p = 0.02$, $\eta^2_p = 0.25$), and a significant three-way interaction between POSITION, DIGIT, and BODY PART ($F(1,20) = 82.93$, $p < 0.0001$, $\eta^2_p = 0.81$). The main effect of BODY PART and significant three-way interaction again verifies that the fingers and toes hold different spatial information.

8.4. Discussion

We investigated the existence of standard body-space relationships in two different body parts: the fingers and the toes. We showed that localisation of tactile stimuli was more efficient (faster RTs and lower error rate) when the thumb is in a relative bottom position, and the middle finger in a relative top position. This provides a

clear replication of the pattern of results reported by Romano and colleagues (in press) when the thumb and middle finger were tested. Moreover, our findings showed that the toes do not share the same standard body-space associations as the fingers – localisation of tactile stimuli was faster on the middle toe regardless of whether it was in the top or bottom position, and error rate was lower for the middle toe in a relative bottom than top position, and for the big toe in a relative top than bottom position (the inverse to results found on the hand). These results provide evidence that standard body-space relationships are *not* a general feature of the representation of the limbs, as patterns of results across the hands are not replicated across the feet. Our results instead suggest that standard representations of the limbs may be learned from frequent actions or postures.

Natural use relationships have already been shown to be related to other somatosensory functions, such as transfer of tactile learning between fingers (Dempsey-Jones et al., 2016) and the representational structure of sensorimotor cortex (Ejaz et al., 2015). The most frequent natural use relationships when grasping using the hand is with the thumb in a relatively lower position than the four fingers (Cutkosky & Howe, 1990; Feix, Romero, Schmiedmayer, Dollar, & Kragic, 2016), which is the same preferential positions found in the present study and by Romano and colleagues (2017; in press). We suggest that natural use relationships from frequent actions or postures, such as grasping objects, may be 'learned' by the somatosensory system as a way to facilitate somatosensory processing for frequently used actions. As the toes are less functionally significant as individual digits than the fingers (which is also reflected in less individuation between toe representation than finger representation in primary

somatosensory cortex; Akselrod et al., 2017; Hashimoto et al., 2013), this can account for why we find strong standard body-space relationships for the fingers, but only weak relationships for the toes.

Not only are standard body-space relationships weaker for the toes than the fingers, but there is a different pattern of results over the two body parts. For error rate, the pattern of results was inverted from the hands to the feet. In human and non-human primates, the anatomy of the hip, knee, and ankle joints constrains leg movement and posture in such a way that it is more comfortable for the outer edge of the foot to be angled towards the ground than the inner edge of the foot, resulting in the big toe being in a relative top position and middle toe in a relative bottom position (Marieb, 2012; Webb & Sparrow, 2007). For example, during arboreal locomotion many non-human primates use the toes in these positions (Holowka et al., 2017b; Schmitt et al., 2016). In humans, most frequent seated postures involved the legs being crossed towards the midline of the body (Hewes, 1955; Snijders, Slagter, Vleeming, Stoeckart, & Stam, 1995), again resulting in the big toe being in a relative top position and middle toe in a relative bottom position. As mentioned in the previous paragraph, although this posture may be used as frequently as hand grasping postures, the toes as individual digits in these postures are not functionally significant, insofar as in the overall posture of the leg is. This may explain why learned patterns of body-space associations are weaker for the toes than the fingers, and are only reflected in a weak evidence for error rate but not RT.

RTs for the toes had a different pattern of results to both error rate on the toes and both measures on the fingers – responses were faster to the middle toe regardless of position. Previous studies have shown that tactile localisation is more accurate for the

big toe than the middle toe (Cicmil et al., 2016; Manser-Smith et al., 2018), which suggests that lower RTs are not simply a result of worse ability to localise touch on the big toe than the middle toe. Moreover, error rate in the present experiment did not indicate that participants were simply worse at responding to tactile stimuli on the big toe than the middle toe.

One limitation of the present study was that different response effectors were used in the blocks where the hands and feet were tested. As such, differences in RT and response accuracy between hands and feet may be related to the different response effectors, and not differences in standard associations. We acknowledge that this is a limitation of the present study, but we do not believe that it has significantly influenced our results. Using the heel and toe of the foot, as well as keyboard presses using the fingers, are both typical response effectors used in the literature for cross-modal congruency tasks (Holmes, Calvert, & Spence, 2004; Maravita, Spence, Sergent, & Driver, 2002; Romano et al., in press; Spence, Pavani, & Driver, 2004; Spence, Pavani, Maravita, & Holmes, 2004). Moreover, Romano et al. (2017) showed that standard body-space associations also manifest at the level of implicit conceptual associations, using an Implicit Association Task (IAT). Participants were presented with images of the index finger or thumb, with the word ‘up’ or ‘down’, and were asked respond using a keyboard whether the combination was congruent or incongruent (they were informed prior to starting which words and images were congruent in each block). Participants responded faster when the picture of the thumb was presented with the word ‘down’, and the finger with the word ‘up’ than vice versa, confirming the same association for thumb-down and finger-up as found in the present experiment and other experiments by

Romano et al. (2017; in press). The consistency of these results using a range of testing and response methods suggests that it is unlikely that the findings of the present study result only from a compatibility effect of the response effector and body part tested.

In conclusion, our results support the hypothesis that standard body-space relationships are not a general feature of the representation of the limbs, as patterns of RT and accuracy results are different across hands and feet. Standard body-space relationships are much stronger and more reliable for the hands, suggesting a main role of ontological development and experience of grasping in their development.

Chapter 9: General Discussion

9.1. Summary of main findings

In previous chapters I have described the body of work I conducted during my doctoral studies. In my project I investigated the somatosensory representations of the hands and feet, including how these representations are systematically distorted. I was particularly interested in how representations of the hands and feet are similar or different, and what this can tell us about how representations of these body parts arise. I chose to investigate somatosensory representation of the hands and feet, as they are serially homologous structures (Lewis, 1989; Rolian et al., 2010) yet they have widely different structures (Lewis, 1989; Owen, 1849/2008) and uses (Chou et al., 2009; Holowka & Lieberman, 2018; Hughes et al., 1990) in humans. As a result, similarities in the representations of the hands and feet may suggest a deep functional connection between the genetic development of these body parts, and their somatosensory representations. On the other hand, differences between these two body parts can show how plasticity of the somatosensory cortex can develop through different use patterns. The main objective of my thesis deals with the question of how the somatosensory representations of the hands and feet are distorted, and the similarities and differences in these patterns.

In Chapter 2 I compared tactile mislocalisation of touches on the digits on the hairy and glabrous skin surfaces of the hands and feet. Previous research has shown a consistent pattern of mislocalisations across the hairy skin of the fingers (Braun et al., 2011; Braun, Ladda, et al., 2005; Schweizer et al., 2001, 2000), although this pattern is

slightly different across the hairy skin of the toes (Cicmil et al., 2016). However, I am not aware of any previous studies that have compared the pattern of tactile mislocalisations on the hairy skin to those on the glabrous skin for the same participants. In the two experiments of Chapter 2 I replicated the characteristic pattern of tactile mislocalisations across the hairy skin surfaces of the toes (Experiment 1) and fingers (Experiment 2). I also showed that the pattern of mislocalisations on the glabrous skin surface of the toes and fingers was consistent with the pattern found on their respective hairy skin surfaces. Moreover, I found that there are idiosyncrasies in participants' patterns of mislocalisation that are shared across the two skin surfaces of the toes and fingers. This finding suggests that biases in tactile mislocalisation for the fingers and toes likely arise from representations of the hand/foot in which both skin surfaces are incorporated, as opposed to arising from SI where the hairy and glabrous skin surfaces are represented separately (Merzenich et al., 1978; Nelson et al., 1980). Longo (2014) previously described a body representation occurring in high-level somatosensory processing in which the hand is represented as a fully 3-dimensional, volumetric object, incorporating both skin surfaces. As described by Cicmil et al. (2016), it is possible that the 3-D representations of the hands and feet result in distinct patterns of mislocalisation as the digits are not accurately represented in their width – if each digit is assumed to be of equal width (which they are not), the resulting pattern of mislocalisations across the toes would be consistent with the patterns found by Cicmil and colleagues and in the present study.

Following on from Chapter 2, I used the same experimental paradigm in Chapters 3 and 4 to investigate whether idiosyncratic differences in mislocalisation are

also shared between the hairy skin of the hand and feet (Chapter 3), and between the left and right hands (Chapter 4). In Chapter 3 I showed that idiosyncratic differences in each participants' pattern of mislocalisations were highly consistent across the fingers and the toes. In Chapter 4, I showed that idiosyncratic differences in each participants' pattern of mislocalisations were highly consistent across the fingers of the left and right hands. These results provide support in favour of there being a common representation of the hands and feet, and the left and right hands. Following the findings of Badde, Röder, and Heed (2019), I suggest that these representations may actually be an abstracted representation of the body in higher-level somatosensory representation, which encodes the body in terms of body part, or body side (this idea is discussed further in the following section).

Another line of research investigating tactile localisation looked not at localising touches on the fingers or toes, but on the continuous skin surfaces of the hand and foot. This task is markedly different to localising touch on the fingers and toes, as the digits have distinct boundaries between them, and each digit has a separate representation in SI (Akselrod et al., 2017; Kolasinski et al., 2016; Martuzzi et al., 2014). While researchers have investigated tactile localisation on the two skin surfaces of the hand (Mancini et al., 2011), they have not yet investigated tactile localisation on either skin surface of the foot, to my knowledge. In Chapter 5 I investigated tactile localisation on the hairy and glabrous skin surfaces of both the hands and feet.

Mancini et al. (2011) found that touches on the hairy skin surface of the hand were consistently mislocalised to a more distal and radial location than the actual touch, whereas touches on the glabrous skin surface of the hand were less consistently

mislocalised in a proximal direction. I found the same pattern of biases in localisation as Mancini and colleagues on the hairy skin surface of the hand, however, I found that tactile localisation on the palm of the hand was also biased in a distal and radial direction. My results suggest that there is greater consistency in the direction (although not the magnitude) of tactile mislocalisation across the two skin surfaces of the hand than Mancini and colleagues' results do, in line with them possibly arising from the common representation of the two skin surfaces of the hand described in the previous paragraph. However, I did find that biases were reduced in magnitude on the glabrous skin surface of the hand compared to the hairy skin surface, consistent with the findings of Mancini and colleagues. This further supports that magnitude of bias is attributable to anisotropies in RF shape for the hairy skin – RFs are larger and oval-shaped on the hairy skin surface of the hand, so estimation of location is less accurate than on the glabrous skin surface where RFs are smaller and more rounded (DiCarlo & Johnson, 2002; DiCarlo et al., 1998).

On the hairy skin surface of the foot, I found that touches were consistently mislocalised to a more distal location than the actual touch, consistent with the findings on the hairy skin surface of the hand. However, I found that biases in tactile localisation on the glabrous skin surface of the foot were not consistent with those on the glabrous skin surface of the hand – touches were biased in a distal direction, but also strongly in a radial direction. Distal biases on the glabrous skin surface of the feet were weaker than those found on the hairy skin surface, which is again consistent with the theory that magnitude of bias arises from RF differences across the two skin surfaces. Although RFs of the glabrous skin surface of the foot are smaller and more rounded than of the

hairy skin (like for the hands) there appears to be less difference in size and shape of RFs for the two skin surfaces of the feet than the two skin surfaces of the hands (Vedel & Roll, 1982). This may be a reason why strong radial biases were found on the glabrous skin surface of the foot.

Following my investigation of tactile localisation on the continuous skin surfaces of the hands and feet, in Chapter 6 I investigated perception of tactile size on the hairy and glabrous skin surfaces of the hands and feet. Like tactile localisation, tactile distance perception relies on RFs to estimate the distance between two touches – Longo and Haggard (2011) suggest in their pixel model that tactile distance is simply measured by the number of RFs between the two touched points. As RFs for the hairy skin surface of the hand are oval shaped, a greater number of RFs are counted between two points going across the hand, than two points going along the hand. As such, touches are perceived as farther apart going across the hand than along the hand (Longo & Haggard, 2011). On the glabrous skin surface of the hand, for which RFs are smaller and more rounded, anisotropies in tactile distance perception are reduced (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015) or non-existent (Green, 1982; Longo & Golubova, 2017; Longo & Haggard, 2011).

In Experiment 1 of Chapter 6 I investigated perception of tactile size on the hairy and glabrous skin surfaces of the feet. I found that points going across the foot were perceived as farther apart than points going along the foot, the same pattern of results as found on the hairy skin surface of the hand in the previous experiment by Longo & Haggard (2011). I also found anisotropies in tactile size perception on the glabrous skin surface of the foot in the same direction, and of the same magnitude.

In Experiment 2 I aimed to test tactile size perception on the hairy and glabrous skin surfaces of both the hands and feet in the same participants, so that magnitude of anisotropies could be directly compared across both body parts. I replicated the results of previous studies, that on the hairy skin surface of the hand points were perceived as farther apart when going across the hand than along (Longo & Haggard, 2011), and on the glabrous skin surface of the hand the pattern of results was the same, but reduced in magnitude (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015). On the hairy skin surface of the foot I replicated my own results of Experiment 1, that points were perceived as farther apart when going across the foot than along. However, on the glabrous skin surface of the foot I found the opposite pattern of results to Experiment 1 – points were perceived as farther apart when going *along* the foot than across. This seemed unusual given that in the results of previous studies the direction of anisotropies was always to perceive the body part as wider than it actually is, despite magnitude of biases found differing (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015; Longo & Haggard, 2011). One possible explanation of this finding was that there were carryover effects between the different skin surfaces tested, as in both Experiment 1 and 2 I used an interleaved block design, testing all the skin surfaces of each participant.

As such, in Experiment 3 I used an independent groups design, testing the hairy and glabrous skin surfaces of the feet in two different groups of participants. As in the previous two experiments of Chapter 6, I found that anisotropies in tactile size perception on the hairy skin surface of the foot were biased towards perceiving tactile distances as farther apart when going across the foot than along the foot. Moreover, I found that anisotropies in tactile distance perception were biased in the same direction

on the glabrous skin of the foot, although magnitude of bias was reduced compared to the hairy skin, consistent with some findings on the hand (Fiori & Longo, 2018; Longo, Ghosh, et al., 2015).

In Chapters 5 and 6 I demonstrate that there are a lot of similarities in the somatosensory representations of the hands and feet – the pattern of tactile localisation across the hairy skin surface of the hands and feet is very similar, as is the pattern across the glabrous skin surface. Moreover, anisotropies in tactile size perception also follow a similar pattern across the hairy skin surfaces of the hands and feet, and the glabrous skin surfaces. The results of both of these experiments have been attributed to the properties of RFs across the hairy and glabrous skin surfaces. As I introduced in Chapter 1, the hairy skin surfaces of both the hands and feet have larger and more oval-shaped RFs (Alloway et al., 1989; Brooks et al., 1961; Brown et al., 1975), whereas RFs on the glabrous skin are smaller and more rounded (DiCarlo & Johnson, 2002; DiCarlo et al., 1998). There is evidence that this difference in RF size and shape across the two skin surfaces is also found for the feet (Vedel & Roll, 1982), although RFs on the glabrous skin of the feet are larger than those on the glabrous skin of the hand (Strzalkowski et al., 2018). It is likely that these broad similarities in somatosensory representation through RFs arose through the coevolution of the hands and feet (Rolian et al., 2010), so that glabrous skin surfaces of both body parts are more sensitive than the hairy skin, and therefore can be used to carry out dextrous actions such as grasping for the hand, or balancing for the foot.

In Chapter 7 I used a DSS paradigm like the one used by Tamè et al. (2011) to investigate spatial coding of touch for the left and right fingers, to investigate spatial

coding of touch for the fingers and toes. As described in previous chapters, they concluded from their results that as distractor stimuli presented to 'neighbouring' fingers on the *other* hand, as well as actual neighbouring fingers on the same hand, distrupt ability to detect tactile stimuli, a single representation of the two hands must be being used. In Chapter 7 I showed that distractor stimuli applied to the 'neighbouring' finger when a toe are the target, as well as distract stimuli applied to actual neighbouring toe, disrupts ability to detect touch on the target digit. Detection of touch on a target finger is disrupted when a distractor stimuli is applied to the actual neighbouring finger, but *not* when a distractor stimuli is applied to the 'neighbouring' toe. While this finding appears to provide further support for an abstracted representation of the body, it also demonstrates that specific task requirements or salience of tactile information can alter how this representation is used. As this was a detection task, and tactile stimuli such as the ones presented in this task are more commonly felt on the fingers than the toes, tactile stimuli applied to the fingers may have been prioritised in somatsensory processing. This finding demonstrates how multiple methods of somatosensory processing may be used to fulfill task requirements, and I discuss further how this informs our knowledge of the abstracted body representation in the following section.

Finally, in Chapter 8 I investigated how the posture of the body informs our body representations, as well as our ability to localise touch on the body. In a series of studies Romano and colleagues (Romano et al., 2017, 2019) demonstrated that specific hand postures are actually incorporated into our body representations – the thumb is represented in a relatively lower position than the fingers, and the fingers are represented in a relatively higher position than the thumb. In Chapter 8 I presented an

experiment in which I used an adapted methodology from Romano et al. (2017), to investigate whether the feet also have embedded postures. I replicated the canonical hand posture that Romano and colleagues (2017; 2019) found, but did not find any reliable postural associations for the toes. This finding suggests that postural associations held by the fingers are not a general feature of the limbs that developed through their co-evolution, but instead are learned through frequent actions and postures used throughout our lifetime.

Altogether the findings of my doctoral research demonstrate the wide range of somatosensory processing that is carried out by both the hands and feet, and how different task requirements can engage different body representations. An abstract body representation may be engaged when asked to compare somatosensory information across body parts that do not already have a common representation. On the other hand, tasks such as tactile size perception may not rely on this function so heavily, as more low-level somatosensory representations in RFs execute this function. I suggest that these different representations may have different origins – while an abstract representation of the body may be a beneficial relic of the evolutionary co-development of the hands and feet, postural information incorporated into the representation of a specific body part may develop in our own lifetime.

9.2. Evidence for an abstract body representation

In previous chapters I have described a body of research that demonstrates deep functional connections between the representations of the hands and feet. For example, in Chapter 3 I described how idiosyncrasies in each participants' pattern of

mislocalisations across the fingers are shared with the pattern of mislocalisation across the toes. In Chapter 4, I demonstrated that idiosyncrasies in participants' responses are also shared across the fingers of the left and right hands. In this section I will argue that these shared idiosyncrasies in somatosensory perception may arise from an abstract representation of the body.

In some ways we can think of this abstract representation of the body similarly to how de Vignemont (2010) describes one aspect of body image – it describes categorical relationships between parts of the body, for example, body parts such as the left and right hands, or body side (the left hand and the left foot). So, it is an 'abstract' representation as it is not a veridical map of the body. Whereas a single representation of the hand incorporating both skin surfaces resembles the actual physical structure of the hand, a single representation of the left and right hands, or of the hand and foot, would not reflect the actual body structure. Instead, a single representation of the hands and feet, for example, would necessarily reflect somewhat abstracted information about each body part, such as 'fifth digit' identifying both the pinky finger and smallest toe. This idea of an abstract representation of the body may also be classified by Longo, Azañón, & Haggard (2010) as an aspect of somato*representation*, which they suggest includes abstract knowledge of the body as an object of perception and categorisation. However, these categorisations refer to the body as it is perceived as an external object. I suggest that an abstract representations of the body may also have a sensorimotor function, i.e. a type of body schema (de Vignemont, 2010) or somato*perception* (Longo et al., 2010).

Previous research has suggested that there are abstracted representations of the hands and feet (Badde et al., 2019), as well as the left and right hands (Tamè et al.,

2011), that are used in sensorimotor tasks. Badde et al. (2019) found that when trying to localise touches on the arms and legs, on some trials participants would mistakenly respond that they felt a touch on an unstimulated limb. Erroneous responses were nearly always attributed to a limb on the same body side, or of the same limb type, suggesting that these mislocalisations arose from an abstracted representation of the body encoded into categories of body part and body side. Tamè et al. (2011) proposed a similar explanation for their results – when localising touches on the fingers, touches are mislocalised onto neighbouring fingers on same hand, as well as the 'neighbouring' finger on the *other* hand. They suggested that this effect may have occurred as a result of a high-level body representation that did not distinguish between body-side. These examples show how abstracted representations of the body may be used not only in our semantic knowledge of the body, but in our sensorimotor functions.

The research that I have presented in this thesis also supports the idea of a high-level abstract representation of the body used for somatosensory tasks. As I used the same experimental paradigm and analysis method in the four studies described in Chapters 2, 3 and 4, I can directly compare my results across these studies. Unlike the finding of shared idiosyncratic differences across the two skin surfaces of the hands and feet reported in Chapter 2, idiosyncrasies shared between the hand and foot (Chapter 3), or between the left and right hands (Chapter 4) must necessarily arise from a representation of the body that is not veridical to the actual body representation. By comparing the findings across these chapters, we can better understand when an abstract representation of the body may be employed, and why.

As described in the discussion of Chapter 4, I found that the most idiosyncrasies in performance were shared between the two skin surfaces of the toes, followed by between the two skin surfaces of the fingers (Chapter 2). Higher-order representations of the two skin surfaces of the toes and fingers may be shared to the greatest extent because they reflect the veridical body structure of a 3-D body part, with the two skin surfaces on alternate sides. The fingers of the left and right hands (Chapter 4) shared fewer individual differences in performance than this, although the fewest individual differences were shared between the fingers and toes (Chapter 3). These findings indicate that the representation of the left and right hands is shared to a lesser degree than the hand *or* foot representations, and the hand *and* foot representation is shared to a lesser degree than that. It seems logical that in the abstract representation of the body, the left and right body sides have a stronger similarity in their common representation than the hands and feet, as despite some physical dissimilarities in bone size (Garn et al., 1976; Plato et al., 1980) and overall volume (Kaye & Konz, 1986), the two body sides are mirror-images of one another. In contrast, although the hands and feet are serially homologous (Rolian et al., 2010) they are more physically dissimilar than the left and right body sides are. The findings across these four experiments may show us in what scenarios an abstract representation of the body becomes useful – when performing a sensorimotor task comparing two body parts that may be physically and functionally dissimilar, an abstract representation may compensate for these differences by finding categorical similarities.

The results described in Chapter 7 using a different experimental paradigm may further inform us when and why abstract representations of the body are used. It seems

from my results when detecting touches on the *toes* than an abstract representation of the body is being utilised, in which there is a common representation of the hands and feet. A distractor touch applied to a 'neighbouring' finger disrupts detection of touch to a toe, which may arise from neighbouring representations of these digits in an abstract representation. However, this interference effect is not present when detecting touches on the fingers (with distractor touches applied to the toes). I argue that the different tasks used in Chapter 7 (detection task) and Chapters 3 and 4 (localisation task) may contribute to differing results across the hands and feet in these studies. The detection task used in Chapter 7 required participants to attend to only one of the fingers or toes at any time, however, participants could receive distractor touches on any of the digits. The somatosensory information presented in this task is more commonly felt on the fingers than the toes, making the touches to the fingers potentially more salient and harder to ignore than touches to the toes. As such, compensatory somatosensory processing may have been involved to detect touches on the fingers, resulting in more frequent veridical identification of touches on the fingers than on the toes. In the localisation task used in Chapters 3 and 4, however, there was no competition between attending to different stimuli, and therefore abstract representations of the body parts tested may have been used without any compensatory mechanisms also being employed. As I discussed in the Introduction of my thesis, this demonstrates the complex variation of sensorimotor mechanisms that may be employed on any one task (de Vignemont, 2010; Longo et al., 2010), and the difficulty in understanding how these mechanisms function in isolation of one another (de Vignemont, 2010; Pitron et al., 2018; Pitron & de Vignemont, 2017).

In this thesis I have stated many times that the hands and feet are serially homologous structures that co-developed (Rolian et al., 2010), suggesting that somatosensory representations of these body parts may be highly integrated. An abstract representation of the hands and feet may also have arisen from these common evolutionary and developmental origins. However, it may be argued that their common genetic code simply resulted in extremely similar, but independent representations of these body parts. For example, similarities in somatosensory perception that I have found across my experiments could also be explained simply through similarities in the somatosensory representations of these different body parts that may have arisen through their co-development. I cannot claim that this is *not* true. For example, both the fingers (Kolasinski et al., 2016; Martuzzi et al., 2014) and toes (Akselrod et al., 2017) are represented serially in SI, which may contribute to the confusions between neighbouring digits when localising touches on both the fingers and toes (as described in Chapter 2). Moreover, somatosensory representations of the hands and feet are altered through everyday use and somatosensory plasticity (Johansson, 2004) resulting in some differences in their representations that are reflected in different patterns of somatosensory perception. For example, the distinct patterns of mislocalisations found for the fingers and toes described in Chapter 2, and the finding in Chapter 8 that the toes do not hold spatial information such as the fingers do.

However, neurophysiological evidence also suggests that there may be an abstracted body representation incorporating multiple body parts in higher-cortical areas. Zhang et al. (2017) reported that in the anterior intraparietal cortex there is not strict anatomical segregation of body parts, but there are single neurons that exhibit

mixed selectivity, i.e. overlapping representations of multiple body parts. Interestingly, the interparietal sulcus has also previously been identified as being involved in the semantic knowledge about arrangements of body parts (Corradi-Dell'Acqua, Hesse, Rumiati, & Fink, 2008). The finding by Zhang and colleagues suggests that although some similarities in tactile processing for the fingers and toes may arise from simple similarities in the somatosensory representations, deeper functional connections between body parts such as shared idiosyncrasies may arise from these abstract representations.

In this section I have presented my idea of what an abstract representation of the body may be – a higher-level representation similar to the body schema, that is used for sensorimotor tasks, but which does not reflect the veridical anatomy but abstracted categorical identities such as 'third digit', which may refer to the middle finger on the left or right hand, or the middle toe. I suggest that an abstract representation may be used in somatosensory tasks involving dissimilar body parts as a compensatory mechanism to compare categorical similarities across them. This idea is supported by previous research such as Badde et al. (2019) and Tamè et al. (2011), as well as my own research. It is also supported by neurophysiological evidence of single neurons that support mixed selectivity in higher-cortical areas (Zhang et al., 2017). Further research is needed to explore when exactly an abstract representation of the body may be employed in a task, and to what extent dissimilar body parts can be compared using this mechanism.

9.3. Limitations and future directions

In all my experiments (except the comparison across the left and right hands in Chapter 4) I investigated tactile somatosensory perception only in the left hand and left foot. Previous research of tactile localisation had indicated that biases in somatosensory perception were more exaggerated for the left body side than the right body side (Cicmil et al., 2016; Schweizer et al., 2001), possibly due to the frequency of this being the non-dominant body side. However, studies of other types of somatosensory biases have found that there is no laterality to magnitude of biases. For example, for both proprioceptive maps (Longo & Haggard, 2010) and tactile distance anisotropies (Longo, Ghosh, et al., 2015) have very similar biases on the left and right hands which are strongly correlated between the two hands. As such, my decision to test only the left body side was in some ways arbitrary, but also motivated by the possibility of finding more exaggerated tactile biases.

As such, I cannot conclude from my series of studies whether an abstract body representation generalises to both body sides, although previous research indicates that it does (Badde et al., 2019; Tamè et al., 2011). Badde et al. (2019) in particular showed that mistaken identification of the limbs may occur according to the categories of limb type, or body side, but not frequently confusing both categories (i.e. touch to the left foot was not mistakenly localised to the right arm). Future research may test whether the results found in my studies generalise across both body sides, and moreover, whether multiple categorisations of body parts (i.e. body side, body part) in an abstract representation can interact to produce confusions of body parts such as the left foot and right hand.

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